UNIVERSITÉ DU QUÉBEC À MONTRÉAL

EFFETS DENSITÉ-DÉPENDANTS CHEZ LA BERNACHE DU CANADA NICHANT DANS LE SUD DU QUÉBEC

MÉMOIRE

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AVANT-PROPOS

Ce mémoire est composé de cinq parties. L'introduction générale, rédigée en français, offre une revue de la littérature sur les principaux effets densité-dépendants détectés dans des populations animales ainsi que sur les agents jusqu'à maintenant moins explorés qui ont motivé les différents volets de notre projet. Le choix de la population à l'étude, soit une population de bernaches du Canada (*Branta canadensis maxima*) nichant dans le sud du Québec, est aussi discuté. L'introduction générale se termine par l'énoncé des objectifs principaux de l'étude. Le corps du mémoire est composé de trois chapitres. Les deux premiers chapitres sont écrits sous forme d'articles scientifiques en anglais dans le but de les soumettre pour publication dans des revues scientifiques. Le premier article porte sur les effets densité-dépendants agissant au niveau de la nidification de la bernache du Canada par le biais de l'hétérogénéité de l'habitat, de l'interférence entre couples avoisinants et de la prédation. Le deuxième article porte quant à lui sur l'impact de la densité des bernaches sur la distance de dispersion natale ainsi que sur la sélection du site de nidification par les individus se reproduisant pour la première fois. Le troisième chapitre est constitué d'une courte communication, aussi écrite en anglais, portant sur l'appariement entre frères et sœurs chez la bernache du Canada et le rôle potentiel de la dispersion natale dans ce type d'appariement. Cette courte communication sera publiée en juin 2013 dans le Wilson Journal of Ornithology (volume 125). J'ai participé à la collecte de données de 2010 à 2012 et réalisé l'ensemble des analyses ainsi que la rédaction des trois articles. Jean-François Giroux, en tant que directeur de recherche, a contribué à l'élaboration du projet et a supervisé l'analyse des données ainsi que l'écriture des articles. Pour ces trois manuscrits, je serai donc la première auteure et Jean-François Giroux sera co-auteur. Pour terminer, la conclusion générale du mémoire, aussi écrite en français, revient sur les principaux résultats et conclusions de l'étude et propose des voies de recherche future sur le sujet.

J'aimerais remercier mon directeur de recherche, Jean-François Giroux, pour m'avoir permis de travailler sur un projet aussi intéressant et pour m'avoir conseillée tout au long de ma maîtrise, même lorsque les délais étaient courts. Un grand merci à mes collègues de laboratoire, Cécile Girault et Florent Lagarde, qui ont partagé avec moi les hauts et les bas du travail de terrain et d'analyse de données. Merci aussi à Catherine Pilotte pour m'avoir initiée au projet des

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RÉSUMÉ

Des effets densité-dépendants survenant lors de la croissance d'une population ont le potentiel de réduire cette hausse démographique. De tels effets densité-dépendants peuvent avoir des causes multiples, mais certaines demeurent moins étudiées. Dans cette optique, nous avons analysé les effets de la densité sur le succès reproducteur et la dispersion natale agissant par d'autres mécanismes qu'une limitation de la nourriture. Pour ce faire, nous avons utilisé un suivi sur plusieurs années d'une population de bernaches du Canada (*Branta canadensis maxima*) nichant dans le sud du Québec. Nos résultats montrent d'une part la présence d'effets densité-dépendants négatifs survenant par hétérogénéité de l'habitat au niveau des risques de prédation et d'inondation des nids. D'autre part, une plus forte densité de couples réduisait leur succès reproducteur, probablement suite à de plus importantes interactions agressives entre ces derniers. Finalement, le risque de prédation des nids variait aussi avec la densité de ceux-ci, de façon positive ou négative selon les prédateurs impliqués. Par ailleurs, malgré une hausse importante de la taille de la population au cours de l'étude, le nombre de couples reproducteurs n'avait pas d'effet sur la distance de dispersion natale des oiseaux. Cependant, la densité de nids à plus fine échelle spatiale influençait la sélection du site de nidification de ces bernaches. Les individus nés dans des parcelles caractérisées par une forte ainsi qu'une faible densité de nids lors de l'année de leur première reproduction dispersaient pour s'établir dans des parcelles de densité intermédiaire, suggérant que des effets bénéfiques de la présence de congénères pourraient aussi être présents. Finalement, nous avons examiné le premier cas connu d'appariement entre frère et sœur chez une espèce d'oie. Bien que non directement reliée à la densité, cette situation pourrait avoir été favorisée par une dispersion natale plus faible que la moyenne chez le mâle de ce couple ainsi que par les fréquentes adoptions observées chez ces oiseaux.

Mots-clés : densité, reproduction, dispersion natale, hétérogénéité de l'habitat, interférence, attraction sociale, densité-dépendance, consanguinité.

INTRODUCTION GÉNÉRALE

La croissance d'une population et les effets densité-dépendants négatifs

Les populations animales ont le potentiel de réaliser des croissances démographiques rapides lorsque les conditions environnementales sont favorables. Cependant, la taille d'une population ne peut pas augmenter indéfiniment. D'une part, des variations dans les conditions environnementales telles que la température ou les précipitations peuvent diminuer le taux de croissance d'une population indépendamment de sa densité. D'autre part, le taux de croissance d'une population peut être affecté par des effets densité-dépendants. Au fur et à mesure qu'une population croît et que l'habitat devient occupé, la disponibilité des ressources nécessaires à la croissance de celle-ci diminue (Cain et al. 2008, Begon et al. 2009). Il peut alors y avoir une hausse du taux de mortalité, une baisse du taux de natalité, une hausse de l'émigration ou une baisse de l'émigration. Plusieurs de ces paramètres peuvent également être affectés simultanément par la densité d'individus. Le taux de croissance de la population peut ainsi être diminué lorsque la densité d'animaux augmente (Cain et al. 2008).

Les effets densité-dépendants négatifs ont donc le potentiel de réguler la croissance des populations en diminuant leur taux de croissance à haute densité. Les effets densité-indépendants n'ont quant à eux pas cette capacité puisqu'ils surviennent indépendamment de la densité de la population (Cain et al. 2008, Begon et al. 2009). L'impact des effets densité-dépendants sur la dynamique des populations est donc des plus intéressants. Dans les dernières décennies, de nombreuses études se sont ainsi intéressées aux mécanismes qui pouvaient réduire la croissance des populations à forte densité, mais plusieurs aspects demeurent à étudier davantage.

Effets densité-dépendants abaissant le taux de survie

La croissance démographique d'une population peut d'une part abaisser le taux de survie des individus. Ainsi, il a été trouvé chez de nombreuses espèces animales qu'une

hausse de densité diminuait la survie des adultes ou des jeunes par une plus forte compétition pour la nourriture (Choquenot et al. 1991, Williams et al. 1993, Coulson et al. 1997, Hixon et Jones 2005). Une baisse du taux de survie dans d'autres populations pourrait aussi être causée par une amplification des interactions agressives entre individus à plus haute densité (Buskirk et Smith 1991).

Une hausse de la prédation des individus avec l'accroissement de la densité a aussi la capacité d'affecter le taux de survie. En effet, les individus peuvent devoir prendre plus de risque face à la prédation pour s'alimenter lorsque la compétition pour la nourriture est plus intense (Anholt et Werner 1995). La compétition intraspécifique peut par ailleurs avoir lieu au niveau des refuges contre les prédateurs, qui peuvent venir à manquer pour une population très abondante de proies (Holbrook et Schmitt 2002, Forrester et Steele 2004). Parallèlement, les prédateurs peuvent faire preuve d'une réponse numérique ou fonctionnelle suite à une hausse de densité (Korpimäki 1993, Anderson 2001). Une réponse numérique correspond à une augmentation de l'abondance des prédateurs en réponse à celle des proies, principalement suite à une plus importante reproduction des prédateurs (Rockwood 2009). La densité de prédateurs peut aussi accroître par une immigration de ceux-ci vers les parcelles où les proies sont nombreuses, ce qui est souvent appelé une réponse agrégative pour la distinguer de la réponse numérique due à la reproduction (Sutherland 1996, Begon et al. 2009). Une réponse fonctionnelle représente quant à elle une modification dans le taux de consommation de proies par un individu. Ce taux peut augmenter avec la densité de proies par une plus haute fréquence de rencontres entre prédateurs et proies ainsi que par une spécialisation comportementale chez le prédateur (Rockwood 2009).

Effets densité-dépendants diminuant le succès reproducteur

Une forte densité d'animaux peut aussi affecter les paramètres reproductifs de ceux-ci. En effet, la fécondité des femelles était diminuée dans des populations de mammifères à plus forte densité suite à une plus faible disponibilité de nourriture pour celles-ci (Wauters et Lens 1995, Sand et al. 1996, Stewart et al. 2005). De façon similaire, la date de ponte

d'oiseaux nidicoles était retardée et la taille de celle-ci diminuait avec une hausse de la densité (Both 1998, Wilkin et al. 2006). Ces changements dans la ponte seraient soit un ajustement effectué par la femelle afin de maximiser le nombre de jeunes que le couple peut nourrir en présence de compétition accrue pour la nourriture ou alors une conséquence de la plus faible condition corporelle des femelles. Ces hypothèses sont soutenues par l'observation d'une hausse de la taille de ponte et d'une ponte plus hâtive en présence de nourriture supplémentaire fournie expérimentalement (Drent et Daan 1980, Arcese et Smith 1988). Même chez des espèces nidifuges, une diminution de la taille de ponte a été observée à plus forte densité et serait alors attribuable à un manque de nutriments chez la femelle, dû à la compétition accrue pour la nourriture ou à un comportement d'alimentation diminué par des interactions agressives plus fréquentes au sein de larges groupes se nourrissant ensemble (Cooch et al. 1989, Sedinger et al. 1998).

Une diminution du succès reproducteur moyen d'une population avec une hausse de sa densité peut être causée par deux mécanismes. D'une part, si l'habitat est hétérogène, des sites de moins bonne qualité sont progressivement occupés lors de la croissance de la population alors qu'ils ne l'étaient pas auparavant. Les individus occupant ces sites ont une plus faible fécondité, alors que les individus dans les meilleurs sites conservent leur succès reproducteur élevé. Les paramètres reproductifs moyens de la population diminuent de ce fait au fur et à mesure que la population croît (Andrewartha et Birch 1954, Rodenhouse et al. 1997, McPeek et al. 2001). Une population dans laquelle les individus s'établissent ainsi préférentiellement dans les sites de meilleure qualité connaîtra une hausse démographique beaucoup plus rapide que s'ils étaient occupés de façon aléatoire. La population continuera alors à croître de façon sigmoïde, et ce jusqu'à ce que tous les sites de nidification, ou du moins ceux offrant une qualité minimale requise, soient occupés (McPeek et al. 2001). D'autre part, le succès reproducteur de tous les individus peut être diminué par une plus forte compétition pour les ressources et des interactions agressives plus fréquentes. Les paramètres reproductifs de tous les animaux d'une population diminuent alors uniformément, abaissant de ce fait les paramètres moyens de la population, quoique la variance entre les individus n'est pas aussi grande que sous l'hypothèse d'hétérogénéité de l'habitat (Lack 1967, Fretwell et Lucas 1970, Sutherland 1996). Les études ayant tenté de distinguer la présence de ces deux

mécanismes dans des populations animales ont principalement attribué chacun d'eux à un manque de nourriture. Les effets densité-dépendants découlaient alors d'une occupation accrue de territoires contenant moins de ressources alimentaires dans le cas de l'hétérogénéité de l'habitat (Wauters et Lens 1995, Ferrer et Donázar 1996, Rodenhouse et al. 2003) ou d'une plus forte compétition intraspécifique pour celles-ci dans le scénario d'interférence (Both 1998, Fernandez et al. 1998).

La compétition pour la nourriture est donc une cause importante d'effets densité-dépendants abaissant la survie et la reproduction. Cependant, tout comme d'autres facteurs peuvent affecter la survie des individus, une diminution de la reproduction à haute densité pourrait aussi avoir d'autres causes, bien qu'elles aient été beaucoup moins étudiées. Tout d'abord, dans les cas des animaux ovipares, la prédation densité-dépendante des œufs suite à une réponse numérique ou fonctionnelle des prédateurs a le potentiel de diminuer le succès reproducteur des individus tout comme elle pouvait diminuer le taux de survie des animaux. Une telle prédation densité-dépendante a effectivement été observée dans des études portant sur des nids artificiels de canards et de tortues (Larivière et Messier 1998, Marchand et Litvaitis 2004, Gunnarson et Elmberg 2008, Elmberg et al. 2009). Toutefois, les conclusions tirées de la prédation de nids artificiels ne représentent pas toujours fidèlement la situation pour de vrais nids d'oiseaux (Butler et Rotella 1998, Zanette 2002). En effet, des différences au niveau de nombreux paramètres tels que la dissimulation du nid, l'odeur dégagée par celui-ci et la présence des parents peuvent créer des patrons de prédation différents. Les études portant sur l'effet de la densité de nids réels sur leur risque de prédation sont toutefois peu nombreuses (Bêty et al. 2001, Ackerman et al. 2004).

Par ailleurs, des interactions agressives plus fréquentes entre individus à plus forte densité pourraient aussi diminuer leur succès reproducteur. En effet, la densité d'individus ainsi que les intrusions territoriales augmentent le niveau de stress des animaux chez diverses espèces d'oiseaux, poissons et mammifères (Harvey et Chevins 1987, Contreras-Sánchez et al. 1998, McCormick 1998, Silverin 1998, Nephew et Romero 2003). Or, de plus hauts niveaux d'hormones de stress ont le potentiel d'affecter négativement de nombreux

paramètres reproductifs (Harvey et Chevins 1987, Contreras-Sánchez et al. 1998, McCormick 1998, Salvante and Williams 2003, Saino et al. 2005, Sheriff et al. 2009). Cependant, ce possible lien entre la densité d'individus et une diminution de leur succès reproducteur par interactions agressives demeure peu exploré, particulièrement chez les oiseaux. Finalement, il pourrait aussi y avoir une certaine hétérogénéité de l'habitat au niveau de facteurs autres que la disponibilité de nourriture, tels qu'une différence au niveau de la communauté de prédateurs des nids ou de la dissimulation offerte par le couvert végétal (Sullivan et Dinsmore 1990, Larivière et Messier 1998, Rodenhouse et al. 2003).

Les effets densité-dépendants positifs et un potentiel compromis lors de la dispersion

Une plus forte densité d'animaux dans une population a le potentiel de diminuer l'aptitude des individus de plusieurs façons. Toutefois, même chez les espèces qui ne chassent pas en groupe ou qui n'élèvent pas les jeunes de façon commune, des effets densité-dépendants positifs peuvent aussi apparaître lorsqu'une certaine densité d'individus leur confère des avantages au niveau de la survie ou du succès reproducteur. Essentiellement, un individu au sein d'un groupe peut voir son risque de prédation réduit par effet de dilution ou alors par vigilance et défense collective (Cresswell 1994, Arroyo et al. 2001, Ebensperger et al. 2006). La présence de congénères peut par ailleurs augmenter le taux individuel d'alimentation dans certaines circonstances, soit en permettant aux individus d'abaisser leur taux de vigilance ou alors en favorisant le repérage de nourriture (Fernández-Juricic et al. 2004, Cameron 2005). De façon similaire, la probabilité de prédation des nids peut diminuer avec une hausse de leur densité par dilution du risque ou par détection et défense commune des couples contre les prédateurs (Bêty et al. 2001, Picman et al. 2002).

L'impact de la densité d'individus dans une population animale, et à plus petite échelle dans une parcelle d'habitat, sur leur survie et leur reproduction est donc loin d'être simple. Ces inconvénients et bénéfices possibles de la densité peuvent influencer la sélection de territoires par les individus et leur dispersion au sein d'une population ainsi qu'entre des populations de différentes densités. Par ailleurs, la présence de congénères et leur densité

pourraient être interprétées comme un indice de la qualité du site par les jeunes individus ou les animaux non familiers avec la région, favorisant ainsi l'immigration (Stamps 1988, Doligez et al. 2003). À l'inverse, les individus territoriaux déjà installés dans une parcelle pourraient empêcher les immigrants de s'y installer (Flowerdew 1974, Pulliam et Danielson 1991, Negro et al. 1997). Dans un même ordre d'idées, il a aussi été proposé que l'émigration à plus forte densité, particulièrement chez les espèces résidentes, puisse être rendue plus difficile par les confrontations encourues lors du passage au travers des territoires de congénères (Hestbeck 1982).

Ainsi, des populations ou régions caractérisées par une forte densité étaient parfois caractérisées par un plus haut taux d'émigration vers des régions moins denses alors que la présence de congénères augmentait l'immigration dans d'autres cas (Coulson et al. 1982, Stamps 1987, Fonseca et Hart 1996, Serrano et al. 2004, Ward and Schlossberg 2004, Einum et al. 2006). Similairement, des relations positives autant que négatives ont été trouvées entre la densité d'individus et la distance de dispersion natale (Nilsson 1989, Léna et al. 1998, Forero et al. 2002, Bray et al. 2007). Cette distance représente l'étendue parcourue par les jeunes individus entre leur lieu de naissance et celui de leur première reproduction (Greenwood et Harvey 1982). Il a donc été proposé que la densité pourrait avoir à la fois des effets néfastes et bénéfiques pour les animaux (Kim et al. 2009). Les individus chercheraient alors à s'établir dans des parcelles de densité moyenne afin de maximiser leur succès. Un tel scénario a effectivement été observé chez une espèce aviaire coloniale, le Fou à pieds bleus (*Sula nebouxii*), par Kim et al. (2009). Or, la présence d'un tel compromis au niveau de la densité chez d'autres espèces, notamment des espèces non coloniales, reste à vérifier.

Par ailleurs, l'étendue de la dispersion natale effectuée par les animaux de chaque sexe a le potentiel d'affecter la fréquence d'accouplements entre individus génétiquement apparentés (Greenwood 1980, Lambin 1994, Kerth et al. 2002, Szulkin and Sheldon 2008b). D'une part, la reproduction entre individus qui sont relativement similaires au niveau génétique sans être de la même famille peut être bénéfique en léguant aux descendants des gènes adaptés au milieu (Shields 1982, Edmands 2007). Cependant, l'appariement entre

individus trop apparentés, tels que des membres d'une même famille, peut être néfaste d'un point de vue génétique pour les jeunes de tels couples (Daniels and Walters 2000, Nakadate et al. 2003, Liberg et al. 2005, Edmands 2007). Ainsi, la distance de dispersion natale, elle-même possiblement influencée par la densité d'individus, pourrait de cette façon affecter le succès reproducteur des individus.

Le choix de la population à l'étude

Nous étions d'une part intéressés à étudier l'impact de la densité d'individus sur leur succès reproducteur. Plus particulièrement, nous voulions regarder les effets moins connus de l'interférence entre individus, de la prédation densité-dépendante de nids réels et de l'hétérogénéité de l'habitat à d'autres niveaux qu'aux ressources alimentaires. D'autre part, afin d'approfondir la compréhension des potentiels effets densité-dépendants négatifs et positifs agissant sur la reproduction, nous voulions analyser l'influence de la densité de congénères sur la sélection du site de nidification et la dispersion natale d'une espèce qui n'est pas coloniale, mais qui peut tout de même se reproduire à des densités appréciables.

Pour ce faire, nous avons étudié une population de bernaches du Canada (*Branta canadensis maxima*) nichant dans le sud du Québec. Cette population s'est établie dans la région de Varennes, au nord-est de Montréal, au début des années 1990. Alors qu'il n'y avait que 3 couples reproducteurs en 1992 nichant sur les îles de Varennes (Giroux et al. 2001), on en retrouvait près de 200 en 2007 plus une centaine d'autres sur les îles avoisinantes (J.-F. Giroux, communication personnelle). Cette population a ainsi connu une forte expansion, avec un taux de croissance (λ) de 1.41, entre 1992 et 2000 (J.-F. Giroux, communication personnelle). Ceci a été suivi par un ralentissement du taux de croissance entre 2001 et 2007 ($\lambda = 1.14$), suggérant une certaine stabilisation dans la taille de la population, qui pourrait être causée par des effets densité-dépendants. En effet, les bernaches sont des oiseaux non coloniaux, mais qui peuvent tout de même se reproduire à des densités relativement élevées dans certaines populations (Ewaschuk and Boag 1972, Giroux 1981, Sovey and Ball 1998).

La population de bernaches ne devrait par ailleurs pas être fortement limitée par un manque de nourriture comme le sont souvent les populations d'oies nichant en région arctique (Cooch et al. 1989, Francis et al. 1992, Williams et al. 1993, Sedinger et al. 2001). D'une part, la productivité primaire des écosystèmes aquatiques et terrestres est généralement plus élevée en région tempérée qu'à des latitudes arctiques (Flanagan et al. 2003, Running et al. 2004). De plus, la population à l'étude se nourrit fréquemment dans des milieux anthropiques tels que des pelouses et des champs agricoles présents sur les rives avoisinantes (J.-F. Giroux, communication personnelle). Or, la consommation de grains dans les terres agricoles améliore la condition corporelle des oies par rapport à une alimentation restreinte aux milieux naturels (Gauthier et al. 2005, Doiron 2006). Finalement, la migration automnale des oies est habituellement très exigeante au niveau de la condition corporelle des oiseaux (Owen et Black 1991, Francis et al. 1992). Cependant, les bernaches nichant dans le sud du Québec ne réalisent qu'une courte migration de quelques centaines de kilomètres entre les aires de reproduction et les aires d'hivernage aux États-Unis (Pilotte 2012) et ne devraient donc pas épuiser leurs réserves corporelles.

Cette population était donc idéale pour étudier les effets densité-dépendants agissant sur la reproduction autrement que par un manque de nourriture. De plus, la survie des individus est assez élevée dans cette population (Pilotte 2012), suggérant que la possible réduction du taux de croissance serait due davantage à une diminution du taux de natalité qu'à une augmentation du taux de mortalité. En outre, la recherche et le suivi des nids étaient aisés puisque ceux-ci se retrouvent au sol. La possibilité de marquer les jeunes à la naissance puis les adultes avec des colliers permettant de les identifier individuellement à distance a aussi facilité le suivi des individus et de leur reproduction. Ainsi, le suivi des paramètres de chaque nid réalisé depuis 2003 était idéal pour étudier les effets densité-dépendants agissant sur la reproduction et identifier le mécanisme sous-jacent, soit l'hétérogénéité de l'habitat ou l'interférence entre individus (Rodenhouse et al. 1997, Beja et Palma 2008). L'étude de la dispersion natale et du choix du site de nidification était aussi rendue possible par ce suivi intensif des individus.

Finalement, bien que l'objectif de cette étude était d'améliorer notre connaissance des effets densité-dépendants pouvant affecter une population en forte croissance, les résultats obtenus pourraient être bénéfiques pour la compréhension de la dynamique des populations de bernaches du Canada se reproduisant en milieu tempéré et leur gestion. En effet, les populations de bernaches du Canada ont connu une très forte croissance au cours des dernières décennies dans la région tempérée de l'Amérique du Nord, causant parfois des désagréments pour les résidents des villes avoisinantes (Atlantic Flyway Council 1999, U.S. Fish and Wildlife Service 2005). Or, tout comme pour la gestion d'espèces menacées, il est essentiel d'avoir une bonne connaissance de la dynamique et de la démographie des populations d'espèces surabondantes afin de pouvoir établir des plans de gestion appropriés (Destefano et Degraaf 2003, Adams et al. 2006).

Objectifs de l'étude

Le premier objectif de ce projet, couvert dans le premier chapitre, était d'étudier les effets densité-dépendants agissant sur la reproduction de la population de bernaches du Canada et de tenter de déterminer le mécanisme de densité-dépendance sous-jacent. D'une part, nous avons vérifié à une échelle régionale si des effets densité-dépendants étaient présents par hétérogénéité de l'habitat en comparant les paramètres reproductifs des individus entre deux zones caractérisées par des densités de nids différentes. À une échelle spatiale plus fine, nous avons examiné l'effet de la proximité des nids les uns aux autres sur le succès reproducteur des individus afin de voir s'il y avait interférence entre ceux-ci. Finalement, nous avons étudié l'impact de la densité des nids sur leur risque de prédation.

Le second objectif consistait à évaluer les conséquences de la densité de la population sur les comportements de dispersion natale et de sélection du site de reproduction. Plus spécifiquement, nous avons regardé l'effet de la densité des individus à deux échelles spatiales (environ 60 m et 11 km) sur la distance de dispersion natale des bernaches, ainsi que l'influence de la densité d'individus sur la sélection du premier site de nidification. Ceci fait

l'objet du deuxième chapitre de ce mémoire. Par ailleurs, l'étendue de la dispersion natale a le potentiel d'affecter l'appariement entre individus apparentés et donc leur succès reproducteur, ce qui est discuté dans le troisième chapitre.

CHAPITRE I

DENSITY-DEPENDENT EFFECTS ON REPRODUCTIVE SUCCESS OF TEMPERATE-NESTING CANADA GEESE

ABSTRACT.—Density-dependent effects on reproduction can arise through habitat heterogeneity or increased competition and interference between neighbours. Negative effects have been found in avian populations and these have been mainly attributed to food limitations. In this study, we investigated whether density-dependent effects could result from heterogeneity in habitat suitability, interference among neighbours or predation. We used data from a population of temperate-nesting Canada Geese (*Branta canadensis maxima*) that has undergone an important increase in a food-abundant region. We compared reproductive success of geese between two zones characterized by different nest densities and looked at the effects of nest proximity on the reproductive parameters within each zone. At a broader scale, we found density-dependent effects due to habitat heterogeneity regarding predation probabilities and flooding events. At a finer scale, reproductive output declined with proximity to neighbours, probably due to increased aggressive interactions between pairs. However, total predation probability showed both positive and negative density-dependence, due to differences in predator community between zones. Density-dependent effects were thus lowering reproductive success of temperate-nesting Canada Geese both through heterogeneity in habitat safety and agonistic interference between neighbours as well as positive density-dependent predation in one zone.

Key words: density, reproduction, habitat heterogeneity, interference, predation.

Introduction

Animal population growth can be affected by density-dependent reduction in mean fecundity. As population size increases in a heterogeneous environment, the best breeding sites become occupied, forcing individuals to use habitats of lesser quality. These individuals should have lower reproductive success, whereas animals using good quality sites should maintain their high breeding output (Rodenhouse et al. 1997, McPeek et al. 2001). On the other hand, reproductive success of all pairs can be reduced due to competition for resources or intensified interference among individuals at higher population densities (Fretwell and Lucas 1970, Sutherland 1996).

The effect of breeding density on reproductive parameters in bird populations has received much attention in the last few decades and most explanations have been based on food resources. Reduced reproductive success has been attributed to an increased use of territories with lower food availability or to greater competition for food (Ferrer and Donázar 1996, Both 1998, Fernandez et al. 1998, Rodenhouse et al. 2003). In nidicolous birds, food limitation may affect reproductive success through a deterioration of adults' body condition or a reduction of food availability while rearing nestlings (Both 1998, Wilkin et al. 2006). In nidifugous species, density dependent effects can similarly occur through food deficiency for breeding females or foraging limitation on the brood-rearing sites (Cooch et al. 1989, Sedinger et al. 1998, Williams et al. 1993).

Yet, factors other than food limitation could decrease reproductive output of birds at higher density. First, density could affect reproductive parameters through differential nest predation. Intensified predation can occur as a consequence of numerical or functional responses of predators with increasing nest density (Larivière and Messier 1998, Gunnarson and Elmberg 2008). Alternatively, higher density may reduce individual nest predation through dilution effect or communal detection and defense against predators (Bêty et al. 2001, Picman et al. 2002). Population size could also affect predation occurrence through habitat heterogeneity if some areas suffer higher predation due to local differences in predator

community or vegetation cover (Sullivan and Dinsmore 1990, Larivière and Messier 1998, Rodenhouse et al. 2003). Secondly, greater levels of aggressive interactions among close neighbours could arise at higher densities, resulting in more nest desertion (Giroux 1981, Sovey and Ball 1998).

We used data from a rapidly growing population of temperate-breeding Canada Geese (*Branta canadensis maxima*) established in a food-abundant region in southern Quebec to study density-dependent effects on reproductive parameters resulting from heterogeneity in habitat suitability for nesting, predation and conspecific interactions. We first tested for density-dependent effects at a large scale by comparing goose reproduction between two adjacent zones characterized by different nest density, which we considered an indication of heterogeneity in nesting habitat quality. We hypothesized that the zone where the number of nests showed the greatest increase and that supported higher nest density would be of better quality, resulting in higher reproductive success. Secondly, we studied the effect of nest density on reproductive parameters within each zone to see whether there were density-dependent effects arising at a small scale through interference among neighbours or density-dependent predation. We hypothesized that nesting parameters would be adversely affected by proximity to neighbouring nests due to intensified agonistic interactions. However, since predation can increase as well as decrease with nest densities, we could not submit a directional hypothesis. This study will help to better understand if and how population density can affect nesting success by other means than food limitation.

Methods

Study area

The study was conducted near Varennes (45°40' N, 73°27' W), 15 km northeast of Montreal, Quebec, Canada. A breeding population of Canada Geese became established in the early 1990s and has been constantly growing since (Giroux et al. 2001). The climate is

temperate and the geese nest on a series of islands located in the St. Lawrence River. A first zone, thereafter referred to as the Varennes islands, included four large islands partially connected by marshes where the number of nesting geese steadily increased after the initial establishment. This resulted in a greater density of nests than in the other zone, referred to as the Repentigny islands, characterized by 21 islands, some partially connected, and varying greatly in size. Although a few nests were located in the early 1990s on the Repentigny islands, their number did not start to increase until 2000 and the density still remained lower than on the Varennes islands. The area available for nesting in each zone varied annually depending on water levels of the St. Lawrence River that can greatly fluctuate between years. The nesting cover found on the islands is described in Giroux et al. (2001). The brood rearing areas along the shores of the islands and the mainland are composed of marshes, agricultural lands, parks, and private properties with lawns. In early June, molt migrants arrive in the area and join the breeding population while the birds disperse to nearby areas during the post-breeding period (Beaumont et al. 2013). All birds have left the region by early to mid-December and the breeding birds return in mid-March.

Data collection

Crews of three to four persons conducted systematic nest searches each year between 2005 and 2012 by covering the entire area at 10-day intervals from the beginning of nesting (early April) until the first nests hatched (early May). We recorded nest position with a GPS (± 10 m) and counted and numbered the eggs in each nest. For nests found during laying, we calculated initiation date, that is the date at which the first egg was laid, knowing that egg-laying interval in Canada Geese is around 1.5 days (Cooper 1978). For nests found in incubation, we determined the age of the embryos by floating the eggs in water (Walter and Rusch, 1997) and then calculated initiation date based on the number of eggs laid and the approximated number of days of incubation. If hatching date was subsequently known, we preferentially estimated initiation date by considering an incubation period of 27 days that started the day the last egg was laid (Cooper 1978). We monitored each nest to assess their fate and possible egg loss. We visited the nests at hatching and marked hatchlings with

individually numbered webtags (Lepage et al. 1998). We made a last visit after the family had left the nest to ascertain nesting and hatching success. Since geese have precocial young, we considered that an egg successfully hatched if it produced a gosling that left the nest. We considered that a nest was successful if at least one egg hatched successfully (Cooper, 1978), and hatching success was the proportion of eggs that hatched in successful nests (Török and Tóth, 1988).

Each July, we captured molting and pre-fledging geese during a ten-day period. We drove goose flocks towards a corral net by coordinating the work of people on foot and in boats. We sexed the birds by cloacal examination and fitted a metal U. S. Fish and Wildlife Service legband on all those captured for the first time. We also fitted an individually coded plastic neckband on web-tagged adult-plumaged birds that served as a sample of known-aged geese that could be located subsequently on a nest. Animal handling methods were approved by the UQAM Animal Care Committee (#578 and #716) and conformed to guidelines of the Canadian Council for Animal Care.

Spatial and statistical analyses

We calculated the surface area of each island for each year based on the water level of the St. Lawrence River on the day at which 10% of the total number of nests were initiated, at which point we considered that most pairs had established their territory. The area was calculated with ArcGIS 9.3 software (ESRI 2008) using topographic data provided by Environment Canada, Meteorological Service of Canada, Hydrology and Ecohydraulic Section[1]. We calculated annual nest density on the Varennes and Repentigny islands based on the total area searched and the number of nests found. We also calculated the nearest-neighbour distance for each nest as the distance to the nearest nest that was active at the same time using ArcGIS 9.3 software. A nest was considered active from the date the first egg was laid until the departure of goslings with their parents, desertion by the pair, predation or

[1]Use of data provided by Environment Canada should not be interpreted as an approbation of our analyses by Environment Canada.

flooding of all eggs. If the closest neighbour of a nest was inactive for the duration of activity of that nest, then the distance to the second closest neighbour was calculated and so on. Single nests on an island (all located in Repentigny) were excluded for analyses using nearest-neighbour distance because this distance included large water expanse. We verified which of nearest-neighbour distance or nest density was a better surrogate to nest proximity by correlating these two variables with annual surface area and number of nests in each zone using R 2.15.1 statistical software (R Core Team 2012).

We analyzed the effect of zone (Varennes vs. Repentigny islands) and nearest-neighbour distance on nesting parameters with generalized linear mixed-effects models (GLMMs; Carrete et al. 2008) using R 2.15.1 statistical software with the lme4 package (Bates et al. 2012). We proceeded in two steps. First we evaluated the effect of the nesting zone alone, without considering nearest-neighbor distances. Second, we included both the zone and the nearest-neighbor distance of a nest in a GLMM. This allowed us to assess the impact of the zone while accounting for differences in densities. On the other hand, it also permitted to evaluate the effect of the nearest-neighbor distance on reproductive parameters within each zone. For all analyses, we log-transformed the nearest-neighbour distance to normalize its distribution. The reproductive parameters tested were clutch size (total number of eggs laid), initiation date (with day one attributed to Julian day 83, which was the absolute minimum), nesting success (success or failure), hatching success (proportion of hatched eggs in successful nests x 10 to comply with analysis requirements), number of goslings produced, partial predation occurrence (whether a portion of the clutch was destroyed or removed by a predator or not), total predation occurrence (whether all eggs of a clutch were destroyed or removed by a predator or not) and desertion occurrence (whether the pair abandoned the nest before hatching or not). We also compared flooding occurrences (whether a nest was flooded or not) between zones as an indication of habitat quality. Clutch size, initiation date, hatching success and goslings produced were modeled with a Poisson error structure, whereas nesting success, partial predation, total predation, desertion and flooding were modeled with a binomial error structure. For each of the GLMMs, year of nesting was included as a random factor to account for annual variation in weather conditions and water levels. As part of another study, a certain number of nests were experimentally destroyed in each zone between

2006 and 2011 and were thus excluded from the analyses on nest and egg fate. Selection of the best model for explaining variation of each reproductive parameter was made by backward stepwise removal of non-significant factors based on their p-value, with an α of 0.05. Except otherwise indicated, means are presented ± standard deviation (SD).

In many bird species, poorer territories are often occupied by younger individuals, which have lower reproductive success (Ferrer and Bisson 2003, Penteriani et al. 2003). Using our sample of marked birds, we thus tested whether the age of geese varied between the two zones with a GLMM with a Poisson error structure including year and bird identity as random effects. We also verified if nearest-neighbour distance was affected by age, with a linear mixed-effects model (LMM) with a normal error structure, including year and identity of birds as random effects, using R 2.15.1 statistical software with nlme package (Pinheiro et al. 2012). Since reproductive parameters might vary according to age of female more than that of male, we used age of female for testing differences between zones, whereas we used both males and females to test for an age effect on the nearest-neighbour distance since it is unclear whether both partners are responsible for nest site selection and territory establishment.

Results

Varennes islands always supported about twice the number of nests than Repentigny islands ($t = 4.383$, $df = 14$, $P < 0.001$) even though the two zones had relatively similar total nesting area ($t = -1.736$, $df = 14$, $P = 0.105$). Island surface greatly varied each year according to water levels (Varennes: $r = -0.97$, $N = 8$, $P < 0.001$; Repentigny: $r = -0.99$, $N = 8$, $P < 0.001$). In some years, the surface of the islands was more than double the area estimated in other years (Table 1.1). Nest density was thus negatively related to the available nesting area in Varennes ($r = -0.75$, $N = 8$, $P = 0.03$) and tended to be so in Repentigny ($r = -0.65$, $N = 8$, $P = 0.08$), but was not correlated with the total number of nests (Varennes: $r = 0.53$, $N = 8$, $P = 0.18$; Repentigny: $r = 0.57$, $N = 8$, $P = 0.14$). Nest density was therefore more affected by

physical factors (water levels and thus island area) than by biological aspects (number of nests), which should be more related to density-dependent effects. On the opposite, annual mean nearest-neighbour distance was negatively correlated with nest number at Varennes ($r = -0.88$, $N = 8$, $P = 0.004$) and nearly so at Repentigny ($r = -0.69$, $N = 8$, $P = 0.06$) but not with total area (Varennes: $r = 0.26$, $N = 8$, $P = 0.52$; Repentigny: $r = -0.39$, $N = 8$, $P = 0.34$). We thus feel confident that nearest-neighbour distance, which was greater on the Repentigny than on the Varennes islands ($t = 3.221$, $df = 14$, $P = 0.006$), was a better measure of nest proximity than density per se. The coefficients of variation of the annual mean nearest-neighbour distances were also greater in Repentigny ($118 \pm 42\%$) than in Varennes ($44 \pm 4\%$; $t = 4.946$, $df = 14$, $P < 0.001$), indicating a greater disparity in nearest-neighbour distances among nests in Repentigny.

We first compared reproductive output of Canada Geese between zones without considering nearest-neighbour distances but including year as a random effect. Nest initiation happened sooner in Varennes than in Repentigny (GLMM $z = -5.73$, $N = 2404$, $P < 0.001$; Table 1.2). There were no differences in clutch size, hatching success or partial predation between the zones ($P > 0.40$ for all parameters). Number of goslings/nest was higher in Varennes than in Repentigny (GLMM $z = 8.855$, $N = 2197$, $P < 0.001$) because of the higher nesting success (GLMM $z = 8.269$, $N = 2200$, $P < 0.001$; Table 1.3). Desertion probability was slightly lower on Varennes than on Repentigny islands (GLMM $z = -2.047$, $N = 1769$, $P = 0.041$). Nest flooding was very important in some years due to rises in water levels of the St. Lawrence River, and affected relatively more nests at Repentigny than Varennes (GLMM $z = 2.009$, $N = 2504$, $P = 0.044$). Nest predation was also higher at Repentigny (GLMM $z = 9.140$, $N = 2504$, $P < 0.001$) while there was no difference in the proportion of nests that failed but for which we could not assess a precise cause (GLMM $z = -0.406$, $N = 2200$, $P = 0.685$). The main predators, as identified by marks left on the eggs, were predominantly mammals with some instances of birds. Based on signs and sightings, mammalian predators on Varennes islands were mostly American minks (*Neovison vison*), probably due to the presence of marshes, whereas red foxes (*Vulpes vulpes*) and striped skunks (*Mephitis mephitis*) were more abundant on Repentigny islands. Most islands at Repentigny suffered

from mammalian predation but not all in the same years. The level of predation also varied from year to year, especially on Repentigny islands (Table 1.3).

Next, we compared reproductive parameters of geese nesting in the two zones while accounting for differences in nearest-neighbour distances as well as the effect of year (Table 1.4). Nest initiation happened sooner in Varennes (Julian day 109) than in Repentigny (111) (GLMM z = -5.25, $P < 0.001$) and the probability that a nest was successful was higher on Varennes (0.81) than on Repentigny islands (0.64) (GLMM z = 8.269, $P < 0.001$). The number of goslings produced in a nest was also higher in Varennes (2.8) than in Repentigny (2.2) (GLMM z = 2.743, $P = 0.006$). Total predation probability varied between the two zones but it was in interaction with nearest-neighbour distance (see below). Clutch size, partial predation, desertion and hatching success were similar on Varennes and Repentigny islands ($P > 0.26$ for all parameters).

Finally, we looked at the impact of nearest-neighbour distances on breeding parameters of Canada Geese while considering the effects of zone and year. Shorter distances, which represent higher local nest density, had a significant negative effect on all reproductive parameters except nesting success and partial predation ($P > 0.19$ for the two parameters; Table 1.4). When the nearest-neighbour distance decreased, initiation date happened later (GLMM z = 7.05, $P < 0.001$; Fig. 1.1), clutch size decreased (GLMM z = -2.59, $P = 0.010$), hatching success decreased (GLMM z = -2.46, $P = 0.014$), the number of goslings decreased (GLMM z = -3.630, $P < 0.001$), and the probability of nest desertion increased (GLMM z = 6.469, $P < 0.001$). To appraise the magnitude of these effects, we calculated that a decrease in nearest-neighbour distance from 40 to 10 m resulted in a delayed nest initiation by about 1.4 day, a reduction of clutch size by 0.3 egg, a diminution of hatching success by 37%, a lowering of 0.3 gosling produced, and a desertion probability increased by 9% (Fig. 1.1).

Total predation was affected by both nearest-neighbour distance (GLMM z = -4.895, $P < 0.001$) and zone (GLMM z = 3.282, $P = 0.001$) with an interaction between these two

parameters (GLMM z = 4.787, $P < 0.001$). With a decrease in nearest-neighbour distance from 40 to 10 m, the probability for a nest to be preyed upon decreased by 7% at Repentigny, whereas it increased by 5% on the Varennes islands (Fig. 1.1). There was thus a beneficial effect of nest proximity at Repentigny, while density still had a detrimental effect on reproductive success at Varennes. The two curves representing predation probability in each zone crossed at an x-value (nearest neighbour-distance) of 13 m, with 93% of all nests having a nearest-neighbour distance greater than this value. Therefore, total predation probability was higher at Varennes than Repentigny at very high nest densities (nearest-neighbour distance < 13 m), while for densities characterizing a majority of nests (nearest-neighbour distance > 13 m), predation was higher in Repentigny.

Since data were collected over eight years, some individuals contributed to more than one breeding event. This could induce a pseudo-replication problem if some individuals were always characterized by a low nearest-neighbour distance combined with poor reproductive output or vice versa. We therefore followed the approach developed by Lessels and Boag (1987) and performed a repeatability analysis to examine individual variation in nearest-neighbour distance of neckbanded birds that were monitored during more than one year. Repeatability of nearest-neighbour distance among breeding events was 0.36 ($F = 2.691$, df = 146,299, $P < 0.001$), which can be considered a low value (Harper 1994). This suggests that nearest-neighbour distance was not strongly influenced by individual factors and that a same bird had different nearest-neighbour distances from year to year. We are thus confident that all breeding events can be considered independent units (Wiklund 1996).

Lastly, we found no difference in mean age of breeding female Canada Geese between the two zones (GLMM z = 0.775, N = 594, $P = 0.439$). Moreover, nearest-neighbour distance was not affected by the age of the female (LMM t = 0.679, N = 594, $P = 0.498$) nor of the male (LMM t = -0.497, N = 139, $P = 0.620$). Therefore, results of the analyses that looked at the effect of zone and density cannot be due to differences in age of the birds between the two zones or among nests with different proximity to neighbours within a zone.

Discussion

We found a negative impact of nest density on reproductive success of Canada Geese. On one hand, a higher probability of total predation and flooding at Repentigny made it a zone of lower quality for nesting, thus yielding a lower reproductive success for geese using these islands. Varennes islands annually supported twice the number of nests found on Repentigny islands for a similar surface. Conjointly, even though most marked geese nested in their natal zone, among the birds that did move between the zones there were more departures from Repentigny towards Varennes (25% of geese hatched in Repentigny, N = 53) than the opposite (12% of geese hatched in Varennes, N = 163) (APL and JFG, unpubl. data). The preferential use of Varennes islands by geese together with the higher quality of this zone for nesting therefore provide some support to the habitat heterogeneity mechanism of density-dependence (Rodenhouse et al. 1997). On the other hand, a majority of reproductive parameters were also negatively affected by proximity to neighbouring nests within each zone, probably because of higher levels of aggressive interactions between closely-established pairs. This supports the interference mechanism of density-dependence (Sutherland 1996). Nesting density therefore reduced reproductive output of temperate-nesting Canada Geese both through heterogeneity in habitat safety and through agonistic interference between neighbours. Besides, we found both positive and negative effects of nest density on predation risk in the different zones of the study area.

A majority of nesting parameters studied differed between the zones, were affected by neighbors' proximity or both. First, nest initiation date was delayed at Repentigny compared to Varennes, even when we accounted for nearest-neighbour distances. This should reduce long-term reproductive success of Canada Geese breeding at Repentigny because juveniles that hatched later reach smaller structural size at fledging and have lower survival rate during their first year (Doiron 2006, Pilotte 2012). The low-lying islands that are more susceptible to flooding at Repentigny may limit nest site availability in early spring, thus delaying nest initiation. A delayed nest initiation also occurred for pairs that nested close to each other within a zone. Territorial birds can be stressed by conspecific intrusions, and this can have adverse effects on many reproductive parameters including delayed nest initiation

(Silverin 1998, Nephew and Romero 2003, Salvante and Williams 2003). Antagonistic fights between neighbouring males are common in Canada Geese from the time of nest-site establishment to departure with young. Females also participate in nest defense especially during egg laying and are frequently subject to harassment by neighbours during incubation when their gander is absent or unable to defend them (Ewaschuk and Boag 1972, Cooper 1978, Akesson and Raveling 1982). Both partners may get involved in more aggressive interactions in denser patches, which could retard their nest establishment. The increased stress level might also delay egg laying of females.

Clutch size of Canada Geese did not differ between Varennes and Repentigny and this could be explained by food abundance and age structure. During the pre-laying and laying periods, birds from both zones feed extensively in ploughed and stubble corn fields located on the mainland along the St. Lawrence River (J.-F. Giroux, personal observations). Corn grains represent a rich source of nutrients for geese that can rely upon these exogenous inputs to complete their clutch (Gauthier et al. 2003, 2005). Besides, using a subsample of known-aged individuals, we found no difference in the mean age of female geese between the two zones, which may suggest a similar age structure and therefore similar breeding experience that otherwise, could have affected clutch size and other reproductive parameters. Nonetheless, we found that clutch size decreased as proximity to neighbouring nest increased. Agonistic interactions with neighbours at higher nest density have the potential to increase stress-hormones levels, which in turn can diminish resistance to oxidative stress (Stier et al. 2012). Clutch size could thus be lowered by these stressful interactions since laying capacity is related to oxidative stress resistance (Bize et al. 2008). Moreover, stress-hormones can also reduce egg hatchability (Sàino et al. 2005) and this could also explain why we found similar results for hatching success than clutch size.

The probability that a pair deserted its nest was higher at Repentigny than Varennes but this difference disappeared when the effect of nearest-neighbour distance was considered. Nevertheless, pairs that were closer to their neighbours had a higher desertion probability, again possibly because of increased aggressive interactions with conspecifics. Unfortunately,

we did not monitor the behaviour of geese during laying and incubation. However, nest desertion at higher densities has often been observed in Canada Geese (Cooper 1978, Giroux 1981, Sovey and Ball 1998). An alternative hypothesis for the observed effect of nearest-neighbor distance on desertion probability, as well as on other parameters such as nest initiation date and clutch size, could be that the best individuals in the population are better at keeping competitors at a distance, and are also those capable of higher reproductive output. Yet, we found no effect of neither partner's age on nearest-neighbour distance. Moreover, the repeatability analysis performed showed that this distance was weakly repeatable across years for a given individual, disproving the hypothesis that some geese were always characterized by a higher nearest-neighbor distance while others constantly had smaller distances. Therefore, the observed effect of nearest-neighbor distance on reproductive parameters could not be attributed to differences in individuals' quality and would then represent a true effect of density.

Flooding probability was higher at Repentigny due to island topography, and this could be considered an index of habitat quality. Total predation was also generally higher at Repentigny than at Varennes. However, nests closer to their neighbours on the Repentigny islands had a lower probability of total predation than those more isolated, whereas aggregated nests were more prone to total predation on Varennes islands, especially at very high densities. At Repentigny, main mammalian predators were red foxes, along with skunks in some years. Therefore, geese nesting at Repentigny might gain advantage from nest aggregation in the form of group detection and defense against large predators, a situation not encountered as often by geese nesting at Varennes. Studies of artificial duck nests have generally found an increase in predation with nest proximity (Larivière and Messier 1998, Gunnarsson and Elmberg 2008). However, artificial nests only monitor nest detection by predators without taking into account nest defense by incubating females, which could be important in large birds like geese and be enhanced when nests are closer to each other. In fact, Ringelman et al. (2102) found that natural duck nests established closer to their neighbors had a lower probability of being preyed upon. They suggested that ducks could seek to settle in safer patches or that inexperienced hens could use the presence of conspecifics as an indication of habitat safety. Yet, predators in Repentigny used different

islands in different years, thus making predation risk at a specific site difficult to assess for geese. Besides, geese could use the presence of conspecifics as a sign of patch safety only if predation occurred early in the breeding season. However, only 9% of nests that were preyed upon at Repentigny were destroyed before the third quartile of initiation date for that year (APL and JFG, unpublished data). Preference for safer patches or conspecific attraction in safe patches thus seem unlikely explanations for the negative relationship between nest density and predation probability at Repentigny. At Varennes, on the other hand, predation was positively density-dependent and minks were the most common predators. The positive relationship between nest density and predation might be the result of an area-restricted nest searching behaviour after an opportunistic discovery of a dense patch of prey (Larivière and Messier 1998). Such a response to prey density was demonstrated in another mustelid, the European Polecat (*Mustela putorius*) (Lode 2000).

Partial predation probability did not vary between zones nor was it affected by nest proximity. It was probably the result of avian predators opportunistically stealing an egg when encountering by chance a nest that a female had momentarily left. Closeness with this nest should thus not increase predation risk of neighbours, nor should proximity with other nests effectively protect the unattended nest from a rapid egg stealing. Such opportunistic egg predation by avian predators should also occur equally in both zones.

In general, reproductive output of temperate-nesting Canada Geese was negatively affected by nest density. Although food availability was not measured in this study, we consider that the higher primary production of aquatic and terrestrial ecosystems in temperate regions compared to arctic or sub-arctic ecosystems (Running et al. 2004) and the presence of favorable anthropogenic habitats (Gauthier et al. 2005) should provide enough feeding opportunities for Canada Geese established in southern Quebec to prevent food from being the primary limiting factor. We are therefore confident that the negative density-dependent effects that we detected should not be attributable mainly to food shortage, as proposed by many other studies (Fernandez et al. 1998, Sedinger et al. 1998, Wilkin et al. 2006). They were instead caused by heterogeneity in habitat safety regarding flooding and predation risks

at a broad spatial scale, as well as by agonistic interference between neighbors at a finer scale and positive density-dependent predation in one zone of the study area. Yet, nest density also showed a beneficial effect through a reduction of predation risk in the other zone. Density-dependent effects on reproduction can therefore originate from other means than food limitations, may vary spatially and arise conjointly at different spatial scales.

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Table 1.1: Nesting area available (ha), number of Canada Goose nests, nest density (nests/ha) and mean nearest-neighbour distance (NND, m) ± SD on Varennes and Repentigny islands, Quebec, Canada, 2005-2012.

Year	Varennes islands				Repentigny islands			
	Area (ha)	Number of nests	Nests/ ha	Mean NND ± SD (m)	Area (ha)	Number of nests	Nests/ ha	Mean NND ± SD (m)
2005	99	126	1.27	59 ± 26	117	53	0.45	103 ± 220
2006	104	146	1.41	58 ± 28	125	83	0.66	59 ± 83
2007	103	190	1.85	52 ± 20	124	103	0.83	58 ± 68
2008	50	206	4.12	42 ± 22	77	114	1.48	79 ± 74
2009	71	219	3.07	46 ± 18	89	118	1.33	70 ± 66
2010	132	228	1.73	52 ± 22	169	130	0.77	62 ± 60
2011	122	243	2.00	43 ± 18	156	127	0.81	61 ± 54
2012	104	323	3.11	39 ± 16	126	129	1.02	57 ± 56

Table 1.2: Annual mean values ± SD of initiation date (Julian day), clutch size, hatching success (proportion of hatched eggs in successful nests) and number of goslings produced/nest for Canada Goose nests on Varennes and Repentigny islands, Quebec, Canada, 2005-2012.

Year	Varennes islands				Repentigny islands			
	Initiation date	Clutch size	Hatching success	Goslings/nest	Initiation date	Clutch size	Hatching success	Goslings/nest
2005	109 ± 7	5.2 ± 1.2	0.85 ± 0.19	2.7 ± 2.6	112 ± 9	5.7 ± 1.3	0.84 ± 0.20	2.4 ± 2.7
2006	104 ± 7	5.3 ± 1.2	0.83 ± 0.22	3.8 ± 2.0	106 ± 8	5.4 ± 1.6	0.86 ± 0.18	4.0 ± 2.5
2007	110 ± 6	5.6 ± 1.5	0.81 ± 0.23	4.0 ± 2.2	112 ± 6	5.4 ± 1.7	0.79 ± 0.24	2.1 ± 2.7
2008	114 ± 7	5.1 ± 1.6	0.84 ± 0.22	3.4 ± 2.4	114 ± 8	5.5 ± 1.7	0.85 ± 0.19	3.6 ± 2.6
2009	104 ± 7	5.6 ± 1.1	0.87 ± 0.18	4.3 ± 2.0	106 ± 7	5.5 ± 1.5	0.88 ± 0.17	4.1 ± 2.4
2010	101 ± 7	5.8 ± 1.4	0.89 ± 0.17	4.7 ± 2.1	102 ± 7	5.3 ± 1.6	0.82 ± 0.21	3.9 ± 2.3
2011	105 ± 9	5.8 ± 1.5	0.84 ± 0.19	2.4 ± 2.7	106 ± 8	5.8 ± 1.2	0.81 ± 0.21	1.3 ± 2.2
2012	99 ± 8	5.5 ± 1.4	0.82 ± 0.21	4.1 ± 2.1	100 ± 8	5.3 ± 1.9	0.79 ± 0.25	2.7 ± 2.6

For sample size in each year, see Table 1.

Table 1.3: Fate (%) of Canada Goose nests on Varennes and Repentigny islands, Quebec, Canada, 2005-2012.

Year	Varennes islands						Repentigny islands					
	% of nests						% of nests					
	Hatched	Deserted	Flooded	Depredated	Failed*	N	Hatched	Deserted	Flooded	Depredated	Failed*	N
2005	58	2	24	11	5	123	50	8	32	8	2	50
2006	88	4	1	6	1	109	81	9	0	3	7	58
2007	86	11	0	1	1	136	46	8	0	46	0	78
2008	77	10	7	5	0	150	74	10	2	14	0	99
2009	89	5	0	4	2	193	83	2	1	10	5	103
2010	89	5	0	2	5	199	83	6	0	6	4	112
2011	48	1	39	5	6	221	28	2	50	13	7	121
2012	88	3	0	4	5	321	60	7	1	28	4	127

* The fate of some failed nests could not be determined with certitude due to a combination of infertile eggs, predation, flooding or desertion.

Table 1.4: Results of generalized linear mixed-effects models (GLMMs) assessing the reproductive parameters of Canada Geese nesting in southern Quebec, Canada, 2005-2012. Nearest-neighbour distance (log-transformed; effect of a diminution in distance showed), zone (effect of nesting on Varennes islands showed) as well as their interaction were tested as fixed effects while year of nesting (N = 8) was included as a random factor in each model. Numbers in parentheses represent the sample size for each reproductive parameter. Significant independent factors ($\alpha = 0.05$) are in bold.

Dependent factors (N) Independent factors	Estimate	SE	z	*P*
Initiation date (2404)				
Zone	-0.047732	0.009087	-5.25	**< 0.001**
Nearest-neighbour distance (ln)	0.041921	0.005950	7.05	**< 0.001**
Zone * nearest-neighbour distance (ln)	-0.003300	0.013328	-0.25	0.804
Clutch size (2313)				
Zone	0.01239	0.01911	0.648	0.517
Nearest-neighbour distance (ln)	-0.03353	0.01297	-2.59	**0.010**
Zone * nearest-neighbour distance (ln)	0.03710	0.02782	1.334	0.182
Partial predation (2504)				
Zone	-0.08172	0.13852	-0.590	0.555
Nearest-neighbour distance (ln)	0.09575	0.09023	1.061	0.289
Zone * nearest-neighbour distance (ln)	-0.1860	0.2012	-0.925	0.355
Total predation (2504)				
Zone	3.1413	0.9572	3.282	**0.001**
Nearest-neighbour distance (ln)	-0.5893	0.1204	-4.895	**< 0.001**
Zone * nearest-neighbour distance (ln)	1.2273	0.2564	4.787	**< 0.001**
Desertion (1769)				
Zone	-0.235403	0.212145	-1.110	0.267
Nearest-neighbour distance (ln)	0.73446	0.11353	6.469	**< 0.001**
Zone * nearest-neighbour distance (ln)	-0.2057	0.2682	-0.767	0.443
Nesting success (2200)				
Zone	0.8898	0.1076	8.269	**< 0.001**
Nearest-neighbour distance (ln)	-0.09646	0.07326	-1.317	0.188
Zone * nearest-neighbour distance (ln)	-0.05936	0.16615	-0.357	0.721
Hatching success (1605)				
Zone	0.01801	0.01908	0.94	0.345
Nearest-neighbour distance (ln)	-0.03300	0.01344	-2.46	**0.014**
Zone * nearest-neighbour distance (ln)	0.01709	0.02778	0.615	0.538
Number of goslings (2197)				
Zone	0.39356	0.14349	2.743	**0.006**
Nearest-neighbour distance (ln)	-0.08447	0.02327	-3.630	**< 0.001**
Zone * nearest-neighbour distance (ln)	0.04360	0.03705	1.177	0.239

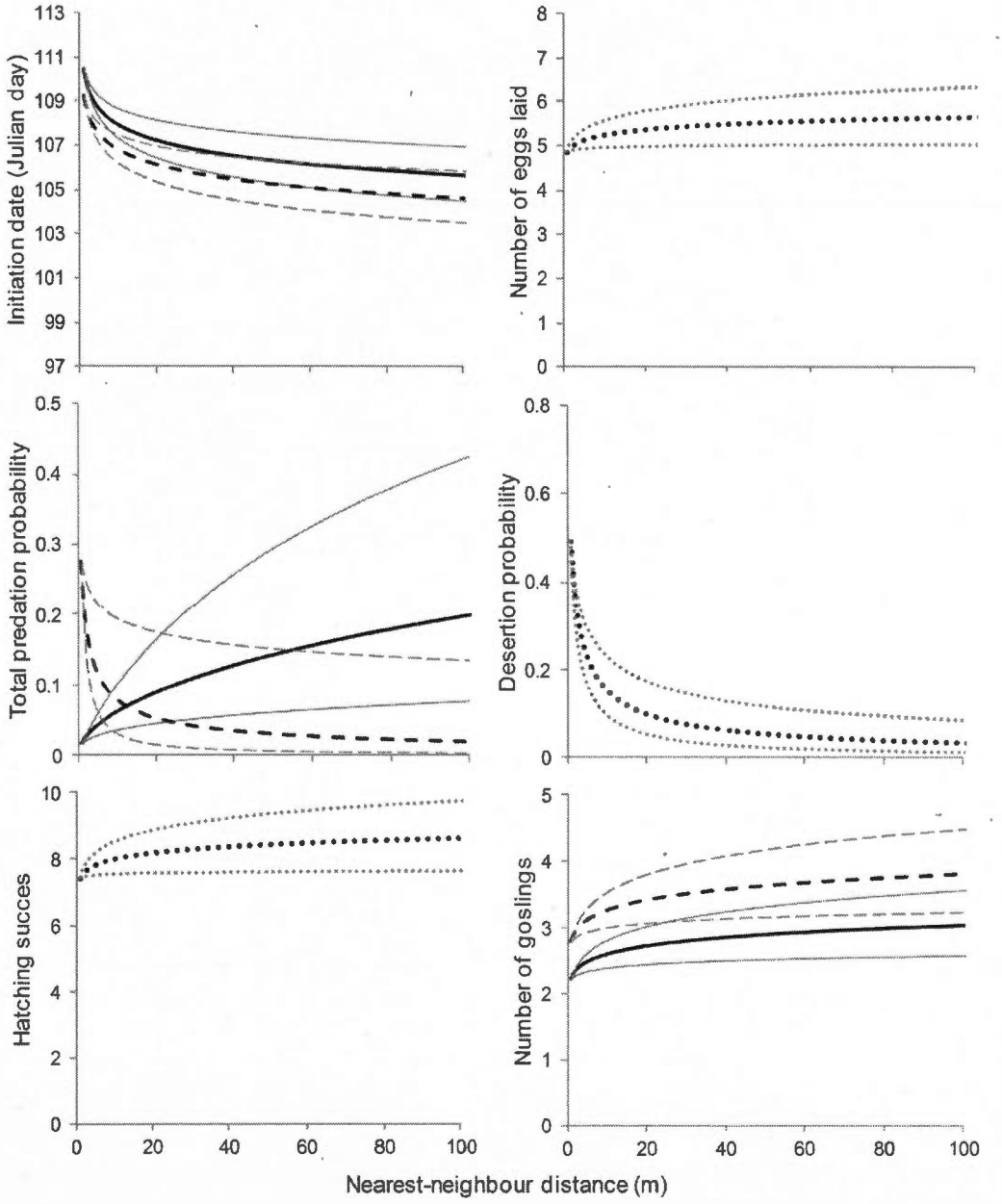

Figure 1.1: Predicted values with 95% confidence intervals of various reproductive parameters of Canada Geese in relation with the nearest-neighbour distance, Quebec, Canada, 2005-2012. Predicted values were obtained from GLMMs with nearest-neighbour distance and zone as fixed factors and year of nesting (N=8) as a random effect. Solid lines are predictions for geese nesting on the Repentigny islands, dashed lines are for geese nesting on Varennes islands, and dotted lines are applicable for geese nesting in both zones.

CHAPITRE II

THE EFFECT OF DENSITY ON NATAL DISPERSAL AND NEST SITE SELECTION IN CANADA GEESE

ABSTRACT.— The influence of conspecific density on natal dispersal in birds has been extensively studied but results are contradictory with both positive and negative effects of density. In some colonial nesting species, the disadvantages and benefits of density can act concomitantly to yield a U-shaped relationship between density and dispersal distance, with new-breeders settling in intermediate-density patches. We used long-term data from a temperate-breeding population of Canada Geese (*Branta canadensis maxima*) nesting on a series of neighbouring islands to investigate the influence of nest density on natal dispersal behaviour and nest site selection. Although Canada Geese are not colonial, they can nevertheless nest at relatively high densities. We found that even if pair number doubled during the study, there was no impact on natal dispersal distances. At a finer spatial scale, we found a negative relationship between potential density (nest density at natal site of a bird in year of its first breeding) and dispersal, probably due to the spatial isolation of low-density patches. We observed that a majority of geese were settling in patches of lower density than their natal one. Yet, birds hatched in patches of low potential density moved to sites characterized by higher nest aggregation. First-time breeders born in sites of high and low potential densities were thus both initiating their nests in similar medium-density patches, suggesting that even though they are not colonial, geese are also subject to both positive and negative effects of conspecific density.

Key words: density-dependence, competition, interference, conspecific attraction, dispersal.

Introduction

Nest site selection by birds can greatly affect their reproductive success (García-Borboroglu and Yorio 2004, Clark and Schutler 1999). Dispersal to a breeding site can thus have significant fitness consequences, and individuals should aim to settle in the most suitable patches (Fretwell and Lucas 1970, Pulliam and Danielson 1991). Natal dispersal generally refers to the movement of an individual from its place of birth to the site of its first breeding attempt, whereas breeding dispersal represents further movements between breeding events (Greenwood and Harvey 1982). Breeding dispersal is usually characterized by shorter movements than natal dispersal, which makes natal dispersal a more decisive process for nest site determination (Greenwood and Harvey 1982, Paradis et al. 1998). Natal dispersal can be influenced by individual attributes including sex, age at first breeding, hatching date, and hatching rank, as well as environmental factors like predation pressure and food availability (Pasinelli et Walters 2002, Byholm et al. 2003, Pasinelli et al. 2004). Social factors such as population density could also influence natal dispersal and nest site selection by recruits, but previous studies have yielded contradictory results. Some showed a positive effect of conspecific density on natal dispersal distance while others revealed an opposite effect or no effect at all (Nilsson 1989, Pärt 1990, Delestrade et al. 1996, Negro et al. 1997, Weelwright and Mauck 1998, Forero et al. 2002).

First-time breeders may seek to return near their natal site as they would have some knowledge of the available resources and the level of predation, which was low enough to have allowed their own fledging (Anderson et al. 1992, Ruusila et al. 2001). However, suitability of a patch for reproduction might decrease as density increases due to higher competition for food, positive density-dependent predation or aggressive interactions among close neighbours (Fretwell and Lucas 1970, Sovey and Ball 1998, Gunnarson and Elmberg 2008). Already established individuals could also prevent new-comers from settling in the best sites, especially if first-time breeders settle later than experienced ones (Jakobsson 1988, Pulliam et Danielson 1991, Negro et al. 1997). As a consequence of intra-specific

competition at higher densities, models predict that birds should leave in search of lower density patches and thus display longer natal dispersal distances (Murray 1967, Waser 1985).

On the other hand, recruits could seek to settle in denser patches since proximity to conspecifics could reduce nest predation through dilution effect or common predator detection and defense (Bêty et al. 2001, Picman et al. 2002). Besides, birds that enter the breeding population could consider nest density as an indication of patch quality (Stamps 1988, Doligez et al. 2003). Conspecific attraction should reduce natal dispersal distance at high density, and has been shown to play a role in nest site selection for species of colonial seabirds, territorial songbirds, birds of prey and, to some extent, for ducks (Pöysä et al. 1998, Serrano et al. 2004, Ward and Schlossberg 2004, Parker et al. 2007).

Finally, it has also been proposed that conspecific density could have both positive and negative impacts on individuals' fitness and thus on dispersal behaviour. In colonial blue-footed Boobies (*Sula nebouxii*), for instance, natal dispersal distance has been found to be longer at low and high densities and shorter at intermediate densities, yielding a U-shaped relationship between density and natal dispersal distance (Kim et al. 2009). Birds hatched in dense patches moved to patches of lower density whereas individuals from low density patches moved to higher density sites. Such a relationship could reconcile hypotheses of both benefits and disadvantages of conspecific density and explain the conflicting results described above. It could also explain the lack of apparent effect of density on dispersal distance found in some studies when a simple linear relationship was used (Pärt 1990). However, besides Kim et al. (2009) no studies have verified whether conspecific density at sites where first-time breeders settle after dispersal is effectively different from what they would experience at their natal site.

The objective of our study was to determine the effects of pair density on natal dispersal and nest site selection in a species that is not colonial but in which conspecifics can nest relatively close to each other. More specifically, we first tested whether natal dispersal distance of Giant Canada Geese (*Branta canadensis maxima*) nesting on a series of

neighbouring islands was affected by the number of pairs in the area. We took advantage of a demographic increase of a local breeding population to look at the effect of density on dispersal at a broad spatial scale. Next, we determined whether the density of pairs at the natal nest site influenced natal dispersal distance at a finer scale. Finally, we compared the density of neighbours at the selected nest site with the density that would have been experienced if the geese had returned to their natal nest sites. Since both positive and negative effects of density on natal dispersal distance were previously found for numerous bird species, with ecological explanations for both scenarios proposed, we could not put forward a clear hypothesis, but whether aimed to verify which one was supported by our data. This study will help to better understand how density can affect dispersal behaviour and nest site selection of non-colonial bird species.

Methods

Study area

The study was conducted near Varennes (45°40' N, 73°27' W), 15 km northeast of Montreal, Quebec, Canada. A few pairs of Giant Canada Geese (*Branta canadensis maxima*) started to breed in the area in the early 1990s and the population has grown rapidly since (Giroux et al. 2001; Pannetier Lebeuf and Giroux in preparation). The geese nest on a series of islands located along an 11.5-km section of the St-Lawrence River (Fig. 2.1). The vegetation covering the islands was previously described by Giroux et al (2001). We limited our search to 25 uninhabited islands that varied in size between 0.1 and 51 ha for a total of 220 ha of nesting habitat. Geese arrive in the area in mid-March and leave the region by early to mid-December.

Data collection

Every year between 2003 and 2012, we conducted systematic nest searches at 10 day intervals over the entire selected area. We recorded the position of each nest with a GPS

(± 10 m). We noted the identity of the pairs attending a nest if they were marked with a neckband. We estimated initiation date as the date at which the first egg was laid. When a nest was found during laying, initiation date was calculated by back-dating from the day the nest was found considering a laying interval of 1.5 days (Cooper 1978). When a nest was found in incubation, we floated the eggs in water to determine approximated numbers of incubation days and calculated initiation date based on embryos age and egg number (Walter and Rusch 1997). We predicted hatching date considering an incubation period of 27 days (Cooper 1978). We visited nests at hatching and marked newly-hatched goslings with individually numbered webtags (Lepage et al. 1998). Each year, we tagged 62-92 % of the goslings hatched on these islands.

Each July, we captured geese by driving goose flocks of molting and pre-fledging birds towards a corral net by the coordinated work of people on foot and in boats. We sexed all birds by cloacal examination. We marked geese captured for the first time with a metal U. S. Fish and Wildlife Service legband and fitted an individually coded plastic neckband on adult-plumaged birds that had a webtag. Animal handling methods were approved by the UQAM Animal Care Committee (#578 and #716) and conformed to guidelines of the Canadian Council for Animal Care.

Spatial and statistical analyses

We used data of geese that were webtagged as goslings, recaptured and fitted with a neckband and subsequently observed attending a nest in the study area between 2005 and 2012. We limited our analyses to two and three year old birds as Giant Canada Geese usually start breeding at these ages (Brakhage 1965, Cooper 1978).

First, we looked for a relationship between natal dispersal distance and the annual number of breeding pairs in the population with a linear mixed-effect model (LMM) using R 2.15.1 statistical software (R Core Team 2012) and the nlme package (Pinheiro et al. 2012). We considered natal dispersal distance as the straight line between the locations of the natal

nest and the first nest initiated by a bird. Natal dispersal distance was log-transformed to normalize its distribution. Sex and age of the birds at first breeding (two or three years old) and initiation date (relative to the annual median) were added to the model along with first-order interactions. Year of nesting was included as a random factor to account for annual differences in surface area of the islands due to fluctuation in water levels of the St. Lawrence River. Since the relationship between density and natal dispersal distance could take a U-shape, we also tested if there was a second-order polynomial relationship between natal dispersal distance and the number of nests recorded each year.

Next, we examined at a finer scale whether natal dispersal distance was influenced by the nest density that first-time breeders would have had if they had returned to their natal nest site (potential density). For nidifugous birds like Canada Geese, it is unlikely that nest density at hatching time could influence natal dispersal. Using density at the natal site in year of first nesting furthermore allows comparisons of nest density between natal and first-nesting sites while avoiding potential problems associated with annual increase in population size (Kim et al. 2009). We used distance to nearest neighbours as a surrogate for nest density as it better reflects the biological reality of nest aggregation (Chapter I). We calculated the mean distance to the three and five closest neighbouring nests that birds would have had at their natal nest site at year of first breeding using ESRI ArcGIS 9.3 software (ESRI 2008). Birds that would have had less than three or five neighbours on their natal island were excluded from analyses since mean distance to nearest neighbours included important water expanse. This led to the exclusion of 4 (2%) and 6 (3%) birds out of 216 for mean distance to the three and five closest neighbours, respectively. We then tested whether potential density influenced natal dispersal distance in a linear and second-order polynomial fashion with LMMs including factors that were found to affect natal dispersal distance. Natal dispersal distance and potential density were log-transformed and year of nesting was added as a random factor to account for annual variations in surface area of the islands.

Finally, we compared nest density at the site where geese first settled (realised density) with the density that they would have experienced if they had returned to their natal

nest site (potential density). We calculated the mean distance to the three and five closest neighbouring nests that birds had at the site of their first nesting attempt using ESRI ArcGIS 9.3 software. Similarly we excluded birds that nested on islands where they had less than three or five neighbours, which represented, respectively, 9 (4%) and 10 (5%) birds. We determined how nest site selection was affected by conspecific aggregation by comparing the realised and potential densities using a paired t-test. We also examined whether the difference between the realised and potential densities was related to the density at the natal nest site during the year when a goose established its first nest (potential density) using a linear model (LM) and including the factors that affected natal dispersal distance. For all analyses, selection of the best model was made by backward stepwise removal of non-significant factors based on their p-value, with an α of 0.05; means are presented ± 1 SE.

Results

No gosling marked with a webtag in 2003 was observed attending a nest in 2005. Between 2006 and 2012, 216 first-time breeders of two (68 females and 27 males) and three years old (91 females and 30 males) were observed at a nest.

Effect of density on natal dispersal distance

Mean natal dispersal distance for males (2193 ± 310 m) was greater than for females (863 ± 111 m) (LMM t = 5.409, $P < 0.001$, N = 213; Fig. 2.2). The maximum natal dispersal distances observed were 8972 and 9572 m for females and males respectively. Age at first breeding and relative nest initiation date had no effect on natal dispersal distance (age: LMM t = 0.702, $P = 0.484$; date: LMM t = 1.053, $P = 0.294$). The total number of nests in the study area increased from 229 in 2006 to 452 in 2012. This represented densities of 0.8 - 2.0 nests/ha over the whole study area, with a range between 0.04 and 111 nests/ha on different islands with two nests or more. At a broad spatial scale, natal dispersal distance was not influenced by the total number of nests recorded each year using either a linear (LMM t = -

0.705, $P = 0.513$; Fig. 2.3) or second-order polynomial relationship (LMM t = 1.414, $P = 0.230$). No interactions between population size, sex, age and initiation date were significant.

At a finer scale, natal dispersal distance of geese increased with the mean distance to the five nearest neighbors (LMM t = 3.054, N = 210, $P = 0.003$; Fig. 2.4). This indicates that geese dispersed over shorter distances when the potential density, that is the density that first-time breeders would have encountered if they had returned to their natal nest site, increased. Using the mean distances to three or five nearest neighbors to compute potential densities yielded similar results. Consequently, we present only data based on five neighbors, as it is probably more representative of the pair density in a patch. There was a difference between sexes (LMM t = 5.043, N = 210, $P < 0.001$) but no significant interaction. The second-order polynomial relationship between natal dispersal distance and potential density was not significant (LMM t = 0.684, N = 210, $P = 0.495$).

Effect of density on nest site selection

Using three or five nearest neighbours to compute realised and potential densities yielded similar results, and consequently we only present data based on five neighbours. There were no differences between sexes in neither realised nor potential densities (LMM t = -1.268, N = 200, $P = 0.206$, and LMM t = 0.239, N = 200, $P = 0.812$, respectively, with year of nesting as a random effect).

Realised density expressed as the mean distance to five nearest neighbours (80 ± 3 m) was greater than potential density (63 ± 2 m) (paired-t test: t = -5.614, df = 199, $P < 0.001$). Therefore, first-time breeders generally sought a less crowded patch than what they would have experienced if they had returned to their natal site. However, the difference between the realised and potential densities was inversely related to the potential density, that is the density that a bird would have encountered if it had returned to its natal site (LM t = -9.177, $P < 0.001$, N = 200; Fig. 2.5). There was no interaction with sex (LM t = -0.472, $P = 0.637$). The majority of geese (161/200, 80%) had a mean distance to their five nearest neighbors at

the natal site less than 81 m, which corresponded to the x-intercept. These geese born in patches with high potential density tended to disperse to patches with lower density (positive difference between realised and potential densities; paired t-test t = 8.427, df = 160, $P < 0.001$). On the other hand, birds hatched in patches of low potential density (mean distance to 5 nearest neighbours greater than 81 m) tended to move to patches with a greater pair density (negative difference between realised and potential densities; paired t-test t = -2.766, df = 38, $P = 0.009$). Yet, there was no difference between the realised densities for geese born in patches with high and low potential densities (t = 0.577, df = 198, $P = 0.565$). Therefore, first-time breeders, no matter if they originated from patches of high or low potential density, settled in patches of similar intermediate density.

Discussion

Population size over the study area did not affect natal dispersal distances of Canada Geese. However, conspecific density affected natal dispersal and nest site selection at a finer spatial scale. There was a negative relationship between local nest density at natal site and dispersal distance. Moreover, a majority of geese settled in a patch with a lower density than what they would have experienced at their natal site (potential density). Yet, birds hatched in patches of low potential density moved instead to denser patches. This resulted in first-time breeders hatched in patches characterized by both high and low potential densities seeking to establish their nest in patches of intermediate densities, suggesting that there were both positive and negative effects of conspecific presence.

The overall density observed during our study increased from 0.8 to 2.0 nests/ha, which is comparable to densities found in other populations of temperate-breeding Canada Geese (Hanson and Eberhardt 1971, Giroux 1981). However, we did observe densities greater than 25 nests/ha on some islands, and this corresponds to the range of higher densities reported by other studies (Ewaschuk and Boag 1972, Sovey and Ball 1998). Although not considered a colonial species, Canada Geese can therefore settle at relatively high density, which has the potential to affect natal dispersal and nest site selection.

Natal dispersal distance of Canada Geese was higher for males than for females, which has been found in other Anserinae populations (Lessels 1985, Leafloor 1998, Nilsson and Persson 2001). This difference in dispersal distances between sexes may contribute to reduce close inbreeding (Pannetier Lebeuf and Giroux 2013). Besides, older birds are often considered more dominant and could thus compete more efficiently for nesting territories near their natal site. This should result in shorter natal dispersal distances for older than younger birds (Pasinelli et al. 2004). However, because we limited our observations to 2 and 3 year old geese, age did not affect natal dispersal. Likewise, first-arriving settlers may select high quality sites, leaving the poorer ones for late-settlers, which would have to disperse further away (Askenmo 1984, Negro et al. 1997). Yet, we failed to find an effect of initiation date, a surrogate for arrival date (Bêty et al. 2003), on natal dispersal distance. It is possible that dominance status and persistence in aggressive interactions over territories were more important than arrival date when competing for the best nest sites (Jakobsson 1988).

The population that we studied underwent an important demographic increase since its establishment in the early 1990s and even doubled during our study. However, we found no effect of population density on natal dispersal distance of individuals at a broad scale, which agrees with other studies (Pärt 1990, Weelwright and Mauck 1998). The overall density of this goose population might still be under a critical threshold that would force the birds to disperse further. The use of a series of islands for nesting might also reduce density-dependent effects on natal dispersal distances since these distances include important water expanses separating nesting grounds. Like most studies on dispersal, ours was limited by the extent of our study area, which consisted in a series of islands within an 11.5-km section of the St. Lawrence River. However, 89% of the natal dispersal distances were less than a third of the potential maximum distance. Moreover, among the 307 geese marked with a webtag and a neckband and observed at a nest since 2005, only four birds have been reported nesting outside the study area despite an extensive network of observers. Although we cannot discard the possibility that some birds may have dispersed over longer distances, we are confident that our data were adequate to study the effects of conspecific density on natal dispersal.

At a finer spatial scale, we found that natal dispersal distance decreased as the potential breeding pair density at the natal site during the year of nest establishment increased. This was most likely the result of low-density patches being more isolated within the study area, although the precise reasons why some islands or parts of islands were avoided by geese remains unclear. Results on nest site selection showed that young geese were seeking to settle in patches of intermediate density. Birds born in patches of low potential density probably had to move greater distances to reach these suitable nesting sites than did geese hatched in patches characterized by higher potential density. Natal dispersal distance was thus affected to some extent by conspecific density at natal site, but likely even more by spatial distribution of the islands and patches of different nest density. This may explain why we did not detect a U-shaped relationship between nest density and natal dispersal as reported by Kim et al. (2009) for Blue-footed Boobies, even though Canada Geese were similarly attracted to medium-density patches.

Nest density measured as the mean distance to nearest neighbours varied within the study area and this affected nest site selection of Canada Geese breeding for the first time. Birds usually established their nest in patches of intermediate nest density rather than in patches of high or low density, suggesting that there were both benefits and disadvantages of conspecific proximity. On one hand, a majority of geese moved to zones that where less crowded than their natal one. This could be the result of birds actively seeking to settle in patches where nests were less aggregated, which should favour higher reproductive success (Chapter I). Besides, Canada Goose males often engage in displays and fights when defending their territory at the beginning of the breeding season, with resident males usually winning (Cooper 1978). Older birds already established in the denser zones could therefore hinder settlement of new-breeders (Cooper 1978, Negro et al. 1997).

Inversely, geese that hatched in patches with low potential density moved to breed in more densely occupied patches. They may thus gain some benefits from establishing their nest in a patch already occupied by other breeding pairs. Nesting close to neighbouring nests may enhance nest defense against mesopredators like red foxes (*Vulpes vulpes*) (Chapter I).

Besides, young birds of different species seem to use density as an indication of territory quality when selecting their first nesting site (e.g. Ward and Schlossberg 2004, Parker et al. 2007). Such conspecific attraction might also play a role in nest site selection by new-breeder Canada Geese and be responsible for the movement of birds from patches of low potential density to patches of higher density.

In conclusion, natal dispersal distance of Canada Geese was not influenced by population density over the study area, but was negatively affected by local nest density at a finer spatial scale, although the spatial distribution of the islands and nest patches was possibly as important. Besides, first-time breeders born in patches of both high and low potential densities tended to move to medium-density patches. This result is similar to what was found for colonial Blue-footed Boobies (Kim et al. 2009) and suggests that even non-colonial birds can be subject to both beneficial and detrimental effects of conspecific density.

Acknowledgments

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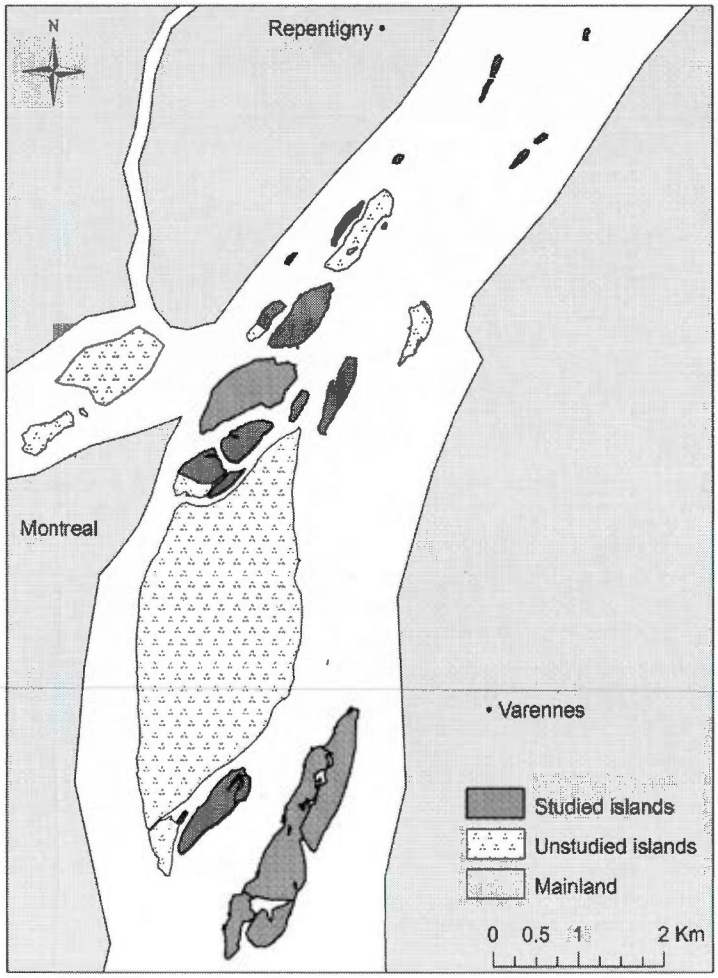

Figure 2.1: Map of the islands searched for Canada Goose nests in southern Quebec, Canada, 2003-2012.

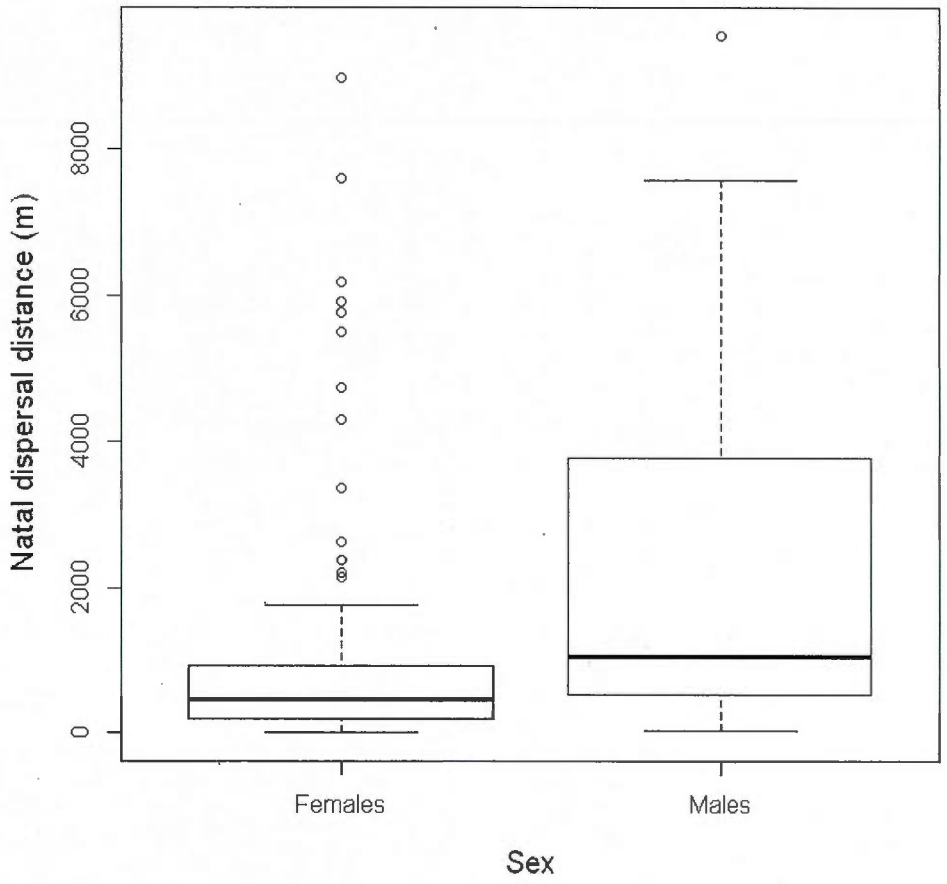

Figure 2.2 : Box-plot of the natal dispersal distance of female (N = 156) and male (N = 56) Canada Geese in southern Quebec, Canada, 2006-2012.

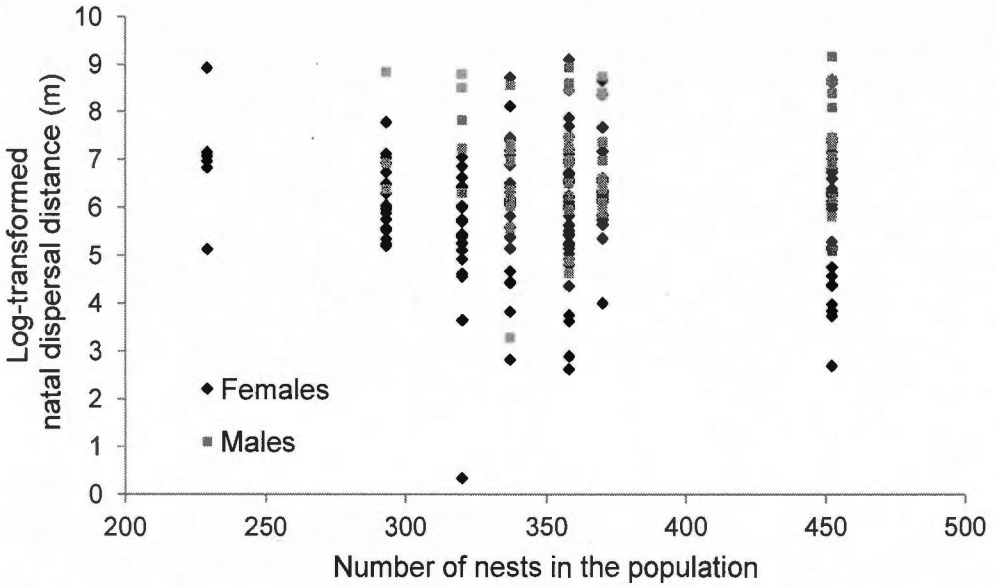

Figure 2.3 : Natal dispersal distance (m; log-transformed) of female (N = 156) and male (N = 57) Canada Geese in relation with the number of breeding pairs at year of recruitment in the population in southern Quebec, Canada, 2006-2012.

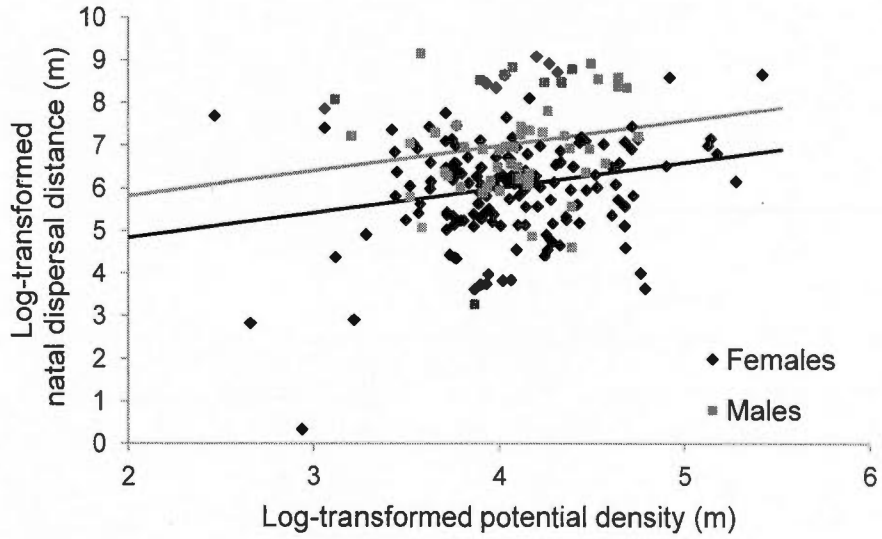

Figure 2.4 : Natal dispersal distance (m; log-transformed) of female and male Canada Geese in relation with the potential density at their natal site in year of recruitment expressed as the mean distance to five nearest neighbours (m; log-transformed), in southern Quebec, Canada, 2006-2012 (Females : y = 3.67 + 0.59 x, N = 155; Males : y = 4.65 + 0.59 x, N = 55; P = 0.013, with year as a random effect).

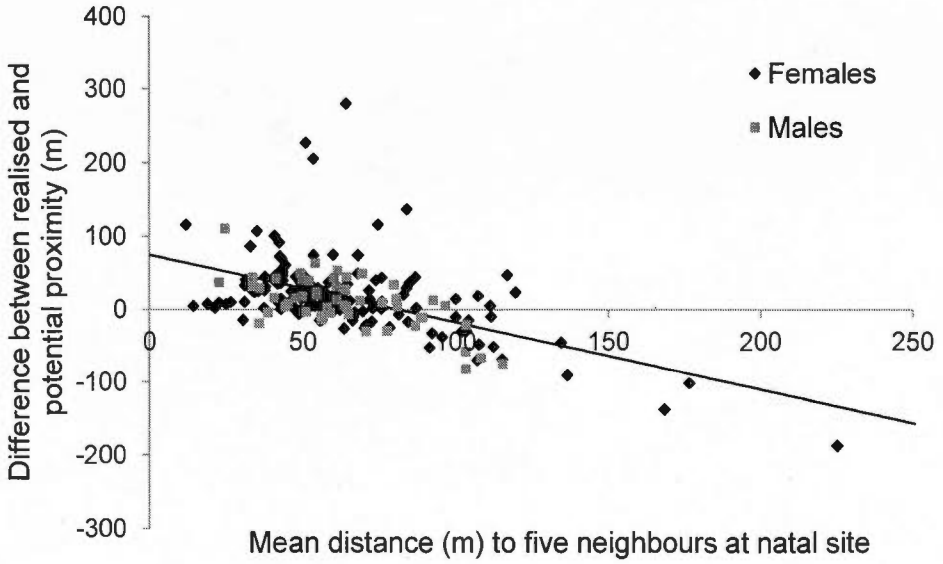

Figure 2.5 : Difference between realised and potential densities (expressed as the mean distance to the five closest neighbours (m) at first nesting site and natal site in year of first breeding) of female and male Canada Geese in relation with the potential density (m) at their natal nest site in southern Quebec, Canada, 2006-2012 ($y = 75.28 - 0.93x$, $r = -0.55$, $N = 200$, $P < 0.001$).

CHAPITRE III

SIBLING PAIRING IN TEMPERATE-NESTING CANADA GEESE

ABSTRACT.—As part of monitoring a population of Canada Geese (*Branta canadensis maxima*) in southern Quebec, two siblings hatched in the same nest in 2008 were later observed breeding together. The geese were first seen as a pair in spring 2011, and we found their nest the following year 437 m from their natal nest site. The sibling pair had lower hatching success than other pairs of the same age cohort. To our knowledge, this is the first report of sibling pairing in the wild for a goose species. Adoption is common in geese, and siblings reared in different family groups may be unfamiliar to one another, which may be the case for the observed sibling pair. Since geese are perennial monogamous birds, full siblings are produced each year, providing further possibility for inbreeding, but we found no pairing among siblings of different ages. Natal dispersal was more important for males and this could contribute, with kin recognition, to inbreeding avoidance.

Key words: Canada Goose, inbreeding, inbreeding avoidance, natal dispersal, sibling pairing.

Introduction

Inbreeding can be viewed as pairing between partners that share ancestors or that are more genetically related than two individuals randomly chosen in a population or meta-population (Keller and Waller 2002). Inbreeding can therefore occur at various levels, with different consequences (Chesser and Ryman 1986). At one end of the continuum, there can be moderate levels of inbreeding between individuals that are not close family but still genetically related, originating from a same population or sub-population of limited size. Such low level of inbreeding can be beneficial through maintenance of co-adapted or locally adapted genes (Shields 1982, Edmands 2007). At the other end, there can be pairing between family members, which is the phenomenon often referred to as inbreeding. Such close inbreeding can cause a reduction in fitness, or inbreeding depression, because of the inferiority of homozygotes or the accumulation of deleterious recessive genes (Edmands 2007). Studies on different bird species have found that reproductive success was generally lower for closely inbred couples (Daniels and Walters 2000, Szulkin and Sheldon 2008a).

Close inbreeding could be prevented by reducing possible encounters with relatives through sex-biased natal dispersal or by kin-recognition (Keller and Arcese 1998). Mating between full siblings is rare in wild bird populations, and most occurrences have been attributed to shorter than average natal dispersal (Greenwood et al. 1978, Carlson et al. 1998, Szulkin and Sheldon 2008b). In this paper, we report the first occurrence of sibling pairing and nesting in the wild for Canada Geese.

Methods

Observations were conducted near Varennes (45° 40' N, 73° 27' W), 15 km northeast of Montreal, Quebec, Canada where a breeding population of Canada Geese (*Branta canadensis maxima*) became established in the early 1990s and has been growing rapidly since (Giroux et al. 2001). In 2012, 450 pairs of geese nested on a series of islands that cover

approximately 250 ha. Between 2003–2010, we marked 4774 hatching goslings with numbered webtags, which enabled us to identify the natal nest site of pre-fledged juveniles recaptured during mass banding operations (5–22 catches per year). We then sexed all birds by cloacal examination and fitted them with US Fish & Wildlife Service metal bands. We also marked 783 adult plumaged birds that had a webtag (428 females and 355 males) with individually coded plastic neckbands. Each spring, we conducted regular observations throughout the breeding area to determine nest location of marked birds. Up to 2012, we observed 307 of these neckbanded geese at nests, including 179 pairs with marked females, 46 with marked males and 41 with both.

Observations

In 2012, we found a nest attended by two birds hatched in the same nest in 2008. Four goslings had hatched in the original nest and all four were webtagged. Two juveniles (a male and a female) were captured together later in the summer and never recaptured. A third bird was captured in another catch, sexed as a male and banded. It was recaptured in 2009 and fitted with neckband H2X6. The last juvenile was captured as an adult female in 2010 and fitted with neckband F6C2. These two neckbanded birds were observed in distinct groups, approximately 10 km apart, on the same day in July 2010. Between April–July 2011, we observed H2X6 and F6C2 in the same group on nine occasions including four instances when they were behaving as a pair. We did not observe them on a nest, but 40% of the goose nests were flooded that year because of high water levels. Both geese were recaptured together during molt in 2011when we confirmed their band and webtag numbers. In 2012, we observed the pair attending a nest 437 m from their natal nest, on the same island. This site had been flooded in 2011, and we suspect that we may have missed their nest. The two geese were recaptured together during mass banding in 2012 and were observed on nine occasions in the same group, including six instances when we recorded them as a pair.

The female of this sibling pair laid her first egg on 10 April, three days later than the mean initiation date for 4-year old females nesting in the area in 2012 (mean ± SE = 7 April ± 1.5, n = 25). She laid five eggs, which was one less than the mean clutch size for comparable females (6.0 ± 0.3, n = 25). Only one egg hatched (20%) compared to 80 ± 10% for other birds of her cohort (n = 21). The other four eggs were either infertile or contained a dead embryo, since at least two of them were liquid inside and none hatched even though the female kept on incubating after hatching of the first egg. The gosling produced was marked with a webtag and was seen near the nest on our last visit 3 days after hatching, but it was not recaptured during banding operations in 2012.

Discussion

To our knowledge, this is the first report of sibling pairing in the wild for a goose species. This record represents a minimum of 0.4% of the breeding pairs within our local population where we had at least one marked individual (n = 266). Three cases of pairing between broodmates have been observed in Mute Swans (*Cygnus olor*), representing 0.2% of breeding attempts (Coleman et al. 1994). Mating between siblings reached 35% for Mallards (*Anas platyrhynchos*) in captivity, but this may have resulted from artificial conditions (Klint 1978). A few cases of sibling pairings have also been documented for species of Passeriformes, Charadriiformes, and Strigiformes, but they represented only 0.1–1.3% of pairings (Greenwood et al. 1978, Carlson et al. 1998, Keller and Arcese 1998, Cook et al. 2007, Jamieson et al. 2009).

In Barnacle Geese (*Branta leucopsis*), pairing occurs either on the wintering or breeding grounds, and when it happens during winter, the birds often choose a partner they have known earlier in life (Owen et al. 1988, Choudhury and Black 1994, Black et al. 2007). In Canada Geese, pairing also seems to occur both on wintering and breeding grounds (Surrendi 1970). Non-breeding (mostly immature) Canada Geese commonly gather in groups during summer (MacInness 1966, Zicus 1981b), and this might play an important role in pair

formation like it does for Barnacle Geese (Hanson 1965, Leafloor 1998). We found that 41 (15%) of the 266 pairs with at least one marked individual were made up of two marked birds. Among the 41 pairs, 54% had partners of the same age, and 27% had a mate that was 1 year older or younger. Furthermore, individuals from five pairs were captured together in the same group during their first or second summer. It is thus quite possible that mates encounter each other in groups of non-breeding birds.

The proposed advantages of pairing with a familiar individual include earlier bonding as well as a common knowledge of the breeding site (Choudhury and Black 1994). Transmission of co-adapted or locally adapted genes to the offspring is another possibility (Shields 1982, Edmands 2007). However, close inbreeding can reduce fitness, as observed for captive Hawaiian Geese (*Branta sandvicensis*) that were closely inbred (Rave et al. 1998). Accordingly, the sibling pair of Canada Geese that we observed had poor hatching success.

Inbreeding can be prevented either by actively avoiding pairing with kin, or by reducing possible encounters with relatives through sex-biased natal dispersal (Keller and Arcese 1998). Discrimination against kin during pair formation requires that individuals have the ability to recognize relatives. In Barnacle Geese, this is thought to be achieved through familiarity rather than by perception of genetic relatedness (Choudhury and Black 1994). Juvenile Canada Geese are able to recognize parental calls as well as individual broodmates when only a few days old (Cowan 1973, Radesäter 1976). Individual recognition might thus allow Canada Geese to pair with individuals from the same breeding region while avoiding broodmates. However, it has been questioned whether siblings that have known each other as immature birds can still recognize one another as adults (Wheelwright et al. 2006). Family break-up in geese usually occurs well after adult size is attained by juveniles and individuals should thus be accustomed to the adult appearance and calls of their broodmates (Warren et al. 1993, Black et al. 2007). Still, adoption is common in geese, and siblings from the same nest may be unfamiliar to one another if some have been adopted by other families (Zicus 1981a, Black et al. 2007). The fact that we did not capture the two broodmates in the same catch before they fledged could suggest that H2X6 and F6C2 were not reared together and

thus did not recognize each other as siblings. Geese are perennial monogamous birds and may produce many broods of full siblings over their lifetime (Baldassarre and Bolen 1994). Young geese are also likely to be unfamiliar with siblings born in other years, which could lead to close inbreeding. However, no such pairing between siblings of different age was found among our sample of marked birds, perhaps because the majority paired with individuals of the same age.

Differential dispersal between sexes could also reduce pairing among full siblings hatched in the same or different years. In Canada Geese, natal philopatry is either higher for females than for males (Surrendi 1970, Lessels 1985) or equal between sexes (Leafloor 1998). Nonetheless, philopatric males tend to disperse over longer distances than females among the natal breeding grounds (Leafloor 1998). Using our sample of marked birds, we found that 51% of females (220/428) and 25% of males (87/355) came back to breed in the study area ($X^2 = 58.9$, df = 1; $P < 0.001$). Adult males and females have similar annual survival rates (Pilotte 2012), but males lose their neckband at a much greater rate than females, probably after aggressive interactions during territorial defense (0.125 vs. 0.011; APL and JFG, unpubl. data). The proportion of males returning to the area is thus underestimated but probably still less than for females. Regarding the distance between the natal nest and the first nest initiated by 2–3 year old birds that returned to the area, it was greater for males than for females (2193 ± 310 m, $n = 57$ vs. 860 ± 109 m, $n = 159$; $t = 6.328$, $P < 0.001$). Finally, 80% of the pairs made up of two marked birds, nested closer to the natal nests of females than to those of males. The greater natal dispersal of males may thus contribute to reduced inbreeding when the first encounters between future mates occur on the breeding grounds. Only long-term intensive marking programs will allow for the estimation of frequency of sibling pairings and a better understanding of the contribution of kin recognition and sex-biased natal dispersal in inbreeding avoidance.

Acknowledgments

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CONCLUSION GÉNÉRALE

Les effets densité-dépendants pouvant réduire la croissance démographique d'une population sont nombreux (Cain et al. 2008, Begon et al. 2009). Cependant, les impacts possibles de la densité d'individus sur leur reproduction ayant d'autres causes qu'un manque de nourriture sont moins connus. Nous avons donc étudié les effets densité-dépendants agissant sur la nidification d'une population de bernaches du Canada (*Branta canadensis maxima*) se reproduisant en milieu tempéré, où la productivité primaire est plus élevée qu'en région arctique et la présence de champs agricoles est favorable pour la condition corporelle des oiseaux (Running et al. 2004, Gauthier et al. 2005).

Dans le premier chapitre, nous avons montré que la densité assez élevée de couples dans la population avait un effet néfaste sur le succès reproducteur moyen. D'une part, il y avait une certaine hétérogénéité de l'habitat, principalement au niveau de la sécurité offerte par les sites de nidification face aux inondations et au risque de prédation des œufs. Les îles plus sûres étaient préférées par les bernaches, mais des individus se sont tout de même tournés vers le groupe d'îles moins sécuritaires au cours de la croissance de la population, où elles ont obtenu un succès reproducteur plus faible. D'autre part, nous avons décelé des effets densité-dépendants survenant à une plus fine échelle spatiale sur la majorité des paramètres de nidification, probablement suite à des interactions agressives plus fréquentes entre voisins rapprochés. Finalement, la prédation des nids s'est avérée densité-dépendante, mais de façon positive dans une zone de l'aire d'étude et négative dans l'autre. Cette distinction au niveau de l'impact de la densité des nids sur leur risque de prédation est probablement causée par la présence de prédateurs distincts, avec une taille corporelle ainsi qu'un comportement de recherche des nids différents.

Notre étude a ainsi permis de montrer que des effets densité-dépendants abaissant le succès reproducteur moyen d'une population peuvent survenir par d'autres mécanismes qu'une compétition accrue pour les ressources alimentaires. Nos résultats soutiennent par ailleurs les études qui suggéraient que plusieurs mécanismes de densité-dépendance négative

peuvent agir simultanément et à des échelles spatiales différentes (Wauters et Lens 1995, Rodenhouse et al. 2003, Carrete et al. 2006). Bien que les effets densité-dépendants détectés ne semblaient pas être suffisamment importants pour diminuer la croissance de la population de bernaches de façon marquante, ils pourraient s'avérer utiles dans la compréhension de la dynamique de populations d'autres espèces et possiblement même dans leur gestion dans certains cas.

Par exemple, un apport supplémentaire de ressources alimentaires est parfois réalisé pour favoriser la croissance des populations réintroduites ou en difficulté, principalement chez les espèces aviaires (Marzluff et Sallabanks 1998, Ewen et al. 2012). Cependant, de tels ajouts de ressources agrégées entraînent généralement une augmentation considérable de la densité d'individus (voir Boutin 1990 pour une revue d'études sur le sujet). Cette hausse de la densité d'animaux, incluant parfois une forte proportion d'individus non reproducteurs, autour des sites d'ajout de nourriture pourrait alors être néfaste pour la reproduction des animaux, tel que trouvé par Carrete et al. (2006) pour les gypaètes barbus (*Gypaetus barbatus*). Les effets densité-dépendants, notamment causés par interférence entre individus, pourraient alors être pris en compte lors de l'élaboration de tels projets. Notamment, de plus nombreux sites supplémentés en nourriture pourraient favoriser la dispersion des individus et ainsi réduire la compétition et l'interférence entre eux afin de maximiser leur aptitude (Bosè et Sarrazin 2007). Par ailleurs, notre étude suggère qu'il peut être nécessaire de suivre la reproduction des individus dans différentes zones d'un habitat afin de bien caractériser le succès reproducteur d'une population car celui-ci peut varier de façon notable à l'intérieur d'une région assez restreinte même en présence de nourriture abondante.

Dans le second chapitre, nous avons présenté les résultats de l'influence de la densité sur le comportement de dispersion natale des bernaches se reproduisant pour la première fois. Bien que la distance de dispersion natale des oiseaux ne fût pas affectée par la densité de couples reproducteurs dans la population, le choix du premier site de nidification par les bernaches était influencé par la densité des nids à une échelle locale. Ainsi, une majorité d'oiseaux s'installaient dans des parcelles caractérisées par une plus faible densité de nids que

ce qu'ils auraient eu s'ils s'étaient reproduits à l'emplacement de leur nid natal. Ceci corrobore les résultats du premier chapitre qui montraient des effets néfastes de la reproduction à forte densité. Cependant, les bernaches qui étaient nées dans des parcelles où la densité était faible durant l'année de leur première nidification se sont plutôt déplacées vers un site où la densité de couples était plus élevée. Ceci est analogue au comportement de sélection du premier site de nidification qui avait été trouvé chez une espèce coloniale (Kim et al. 2009). Certains bénéfices proposés pour expliquer le développement de la colonialité (voir Danchin et Wagner 1997 pour une synthèse des principales hypothèses) pourraient alors s'appliquer dans une certaine mesure à des espèces non coloniales. La plus faible prédation à forte densité trouvée dans une des deux zones de l'aire d'étude dans le premier chapitre pourrait notamment en être un.

Les résultats de notre étude peuvent d'autre part s'ajouter aux connaissances déjà acquises sur la démographie des bernaches du Canada en milieu tempéré dans l'optique de réaliser une gestion adéquate de cette espèce abondante. La population à l'étude a connu une croissance démographique considérable depuis son établissement, comme c'est le cas pour plusieurs autres aux États-Unis et dans le sud du Canada (Nelson et Oetting 1998, U.S. Fish and Wildlife Service 2005). Les aires d'élevage des jeunes ne semblent pas être limitantes et le taux de survie des juvéniles ainsi que des adultes y est assez élevé (Doiron 2006, Pilotte 2012). Cependant, la hausse du nombre de couples reproducteurs dans la population et leur densité assez forte par endroits ont entraîné une diminution du succès reproducteur des oiseaux, qui pourrait aussi être rencontrée dans d'autres populations semblables. Cette baisse du taux de natalité n'est toutefois pas assez importante présentement pour limiter la croissance de la population, qui continue visiblement de croître. De plus, malgré une hausse importante de la densité globale de la population, les distances de dispersion restent assez faibles et le taux d'émigration semble demeurer bas. Toutefois, la majorité des individus (80%) étaient issus de parcelles ayant une densité supérieure à celle recherchée par les oiseaux nichant pour la première fois. Ceci pourrait suggérer que la densité de la population pourrait prochainement avoir davantage d'effet sur la dispersion des oiseaux ainsi que leur reproduction. La poursuite du suivi de la population pourra permettre de constater les impacts à plus long terme des effets densité-dépendants détectés et leurs répercussions sur la

dynamique de cette population, ainsi que des populations similaires nichant dans la zone tempérée de l'Amérique du Nord.

Finalement, dans le troisième chapitre, nous avons rapporté le premier cas connu d'appariement consanguin chez une espèce d'oie. Comme discuté dans ce chapitre, cet appariement a pu être favorisé par l'adoption d'un des deux individus à un jeune âge, empêchant de ce fait la reconnaissance subséquente de leur lien familial. Une dispersion natale par le mâle plus courte que réalisée habituellement par les individus de ce sexe pourrait aussi avoir contribué à ce cas de consanguinité. La poursuite d'études à long terme dans lesquelles les individus sont marqués individuellement permettra de mieux comprendre l'influence de la dispersion natale, et conséquemment de l'effet de la densité de la population, sur l'occurrence d'appariements consanguins.

En outre, de plus amples informations sur le comportement territorial des individus permettraient aussi de mieux comprendre les effets densité-dépendants observés. En effet, nous pensons que la diminution du succès reproducteur à plus forte densité de nids était causée par des interactions agressives plus fréquentes entre voisins contigus, notamment par une hausse du taux sanguin d'hormones de stress (glucocorticostéroïdes). De telles interactions agonistiques seraient aussi une cause possible de la dispersion des jeunes bernaches vers des parcelles de moins forte densité. Des études antérieures ont montré que les bernaches défendaient vivement leur territoire contre les intrusions par des congénères tout au long de la nidification, et particulièrement lors de la période d'établissement des territoires quand les parades, combats et poursuites étaient chose fréquente (Ewaschuk and Boag 1972, Cooper 1978, Akesson and Raveling 1982). Cependant, il n'a pas pu être confirmé si le taux d'interactions agressives entre couples augmentait bien avec leur densité. Il serait donc des plus intéressants de poursuivre ce travail en vérifiant directement l'impact de la densité sur les interactions entre les oiseaux durant l'établissement des territoires ainsi que tout au long de la ponte et l'incubation des œufs. Une meilleure compréhension de l'impact de l'âge et du statut de dominance des individus sur l'issue de ces interactions serait aussi profitable. De même, une étude qui ajouterait la mesure du taux sanguin de glucocorticostéroïdes à celle de la

densité d'individus et de leurs paramètres reproductifs pourrait également permettre de vérifier notre hypothèse et renforcer notre compréhension des effets densité-dépendants agissant par interférence entre individus sur la reproduction et la dispersion. Une étude expérimentale dans laquelle la densité locale de nids serait manipulée pourrait aussi permettre de vérifier directement les impacts sur le comportement territorial des oiseaux, leur taux sanguin d'hormones de stress et leur succès reproducteur.

Ainsi, les divers volets de notre étude ont permis d'acquérir une meilleure compréhension de diverses manières dont la densité d'une population animale peut influencer le succès reproducteur des individus ainsi que le comportement de dispersion natale des jeunes vers leur premier site de reproduction. Toutefois, beaucoup reste encore à faire afin de mieux saisir de quelle façon les variables environnementales et sociales influencent conjointement l'aptitude des individus et leur disposition spatiale, qui à leur tour affectent la dynamique de la population.

BIBLIOGRAPHIE

Ackerman, J. T., A. L. Blackmer et J. M. Eadie. 2004. «Is Predation on Waterfowl Nests Density Dependent? - Tests at Three Spatial Scales». *Oikos*, vol. 107, no 1, p. 128-140.

Adams, C. E., K. Lindsay et S. J. Ash. 2006. *Urban Wildlife Management*. Boca Raton : Taylor & Francis Group, 311 p.

Akesson, T. R. et D. G. Raveling. 1982. «Behaviors Associated with Seasonal Reproduction and Long-Term Monogamy in Canada Geese». *The Condor*, vol. 84, no 2, p. 188-196.

Anderson, M. G., J. M. Rhymer et F. C. Rohwer. 1992. «Philopatry, Dispersal and the Genetic Structure of Waterfowl Populations». In *Ecology and Management of Breeding Waterfowl*, sous la dir. de D. D. J. Batt, A. D. Afton, C. D. Ankney, D. H. Johnson, J. A. Kadlek et G. L. Krapu, p. 365-395. Minneapolis : University of Minnesota Press.

Anderson, T. W. 2001. «Predator Responses, Prey Refuges, and Density-Dependent Mortality of a Marine Fish». *Ecology*, vol. 82, no 1, p. 245-257.

Andrewartha, H. G. et L. C. Birch. 1954. *The Distribution and Abundance of Animals*. Chicago : The University of Chicago Press, 782 p.

Anholt, B. R. et E. E. Werner. 1995. «Interaction Between Food Availability and Predation Mortality Mediated by Adaptive Behavior». *Ecology*, vol. 76, no 7, p. 2230-2234.

Arcese, P. et J. N. M. Smith. 1988. «Effects of Population Density and Supplemental Food on Reproduction in Song Sparrows». *Journal of Animal Ecology*, vol. 57, no 1, p. 119-136.

Arroyo, B., F. Mougeot et V. Bretagnolle. 2001. «Colonial Breeding and Nest Defence in Montagu's Harrier (*Circus pygargus*)». *Behavioral Ecology and Sociobiology*, vol. 50, no 2, p. 109-115.

Askenmo, C. E. H. 1984. «Polygyny and Nest Site Selection in the Pied Flycatcher». *Animal Behaviour*, vol. 32, no 4, p. 972-980.

Baldassarre, G. A. et E. G. Bolen. 1992. *Waterfowl Ecology and Management*. New York : John Willey & Sons Inc., 609 p.

Bates, D., M. Maechler et B. Bolker. 2012. *lme4: Linear Mixed-Effects Models Using S4 Classes.* R package version 0.999999-0.

Beaumont, M., J. Rodrigue et J. F. Giroux. 2013. «Movements and Habitat Use by Temperate-Nesting Canada Geese during the Post-Breeding Period in Southern Quebec». *Avian Conservation and Ecology*, sous presse.

Begon, M., M. Mortimer et D. J. Thompson. 2009. *Population Ecology: A Unified Study of Animals and Plants. 2e éd.* Malden : Blackwell Science Ltd., 256 p.

Beja, P. et L. Palma. 2008. «Limitations of Methods to Test Density-Dependent Fecundity Hypothesis». *Journal of Animal Ecology*, vol. 77, no 2, p. 335-340.

Bêty, J., G. Gauthier et J.-F. Giroux. 2003. «Body Condition, Migration, and Timing of Reproduction in Snow Geese: A Test of the Condition-Dependent Model of Optimal Clutch Size». *The American Naturalist*, vol. 162, no 1, p. 110-121.

Bêty, J., G. Gauthier, J.-F. Giroux et E. Korpimäki. 2001. «Are Goose Nesting Success and Lemming Cycles Linked? Interplay Between Nest Density and Predators». *Oikos*, vol. 93, no 3, p. 388-400.

Bize, P., G. Devevey, P. Monaghan, B. Doligez et P. Christe. 2008. «Fecundity and Survival in Relation to Resistance to Oxidative Stress in a Free-Living Bird». *Ecology*, vol. 89, no 9, p. 2584-2593.

Black, J. M., J. Prop et K. Larsson. 2007. *Wild Goose Dilemmas: Population Consequences of Individual Decisions in Barnacle Geese*. Groningen : Branta Press, 254 p.

Bosè, M. et F. Sarrazin. 2007. «Competitive Behaviour and Feeding Rate in a Reintroduced Population of Griffon Vultures *Gyps fulvus*». *Ibis*, vol. 149, no 3, p. 490-501.

Both, C. 1998. «Density Dependence of Clutch Size: Habitat Heterogeneity or Individual Adjustment?». *Journal of Animal Ecology*, vol. 67, no 4, p. 659-666.

Boutin, S. 1990. «Food Supplementation Experiments with Terrestrial Vertebrates: Patterns, Problems, and the Future». *Canadian Journal of Zoology*, vol. 68, no 2, p. 203-220.

Brakhage, G. K. 1965. «Biology and Behavior of Tub-Nesting Canada Geese». *The Journal of Wildlife Management*, vol. 29, no 4, p. 751-771.

Bray, Y., S. Devillard, E. Marboutin, B. Mauvy et R. Péroux. 2007. «Natal Dispersal of European Hare in France». *Journal of Zoology*, vol. 273, no 4, p. 426-434.

Buskirk, J. V. et D. C. Smith. 1991. «Density-Dependent Population Regulation in a Salamander». *Ecology*, vol. 72, no 5, p. 1747-1756.

Butler, M. A. et J. J. Rotella. 1998. «Validity of Using Artificial Nests to Assess Duck-Nest Success». *Journal of Wildlife Management*, vol. 62, no 1, p. 163-171.

Byholm, P., P. Saurola, H. Lindén, M. Wikman et C. Marti. 2003. «Causes of Dispersal in Northern Goshawks (*Accipiter gentilis*) in Finland». *The Auk*, vol. 120, no 3, p. 706-716.

Cain, M. L., W. D. Bowman et S. D. Hacker. 2008. *Ecology*. Sunderland : Sinauer Associates Incorporated, 621 p.

Cameron, M. 2005. «Group Size and Feeding Rates of Glossy Black-Cockatoos in Central New South Wales». *Emu*, vol. 105, no 4, p. 299-304.

Carlson, P. C., W. S. LaHaye et A. B. Franklin. 1998. «Incestuous Behavior in Spotted Owls». *Wilson Bulletin*, vol. 110, no 4, p. 562-564.

Carrete, M., J. A. Donázar et A. Margalida. 2006. «Density-Dependent Productivity Depression in Pyrenean Bearded Vultures: Implications for Conservation». *Ecological Applications*, vol. 16, no 5, p. 1674-1682.

Carrete, M., J. L. Tella, J. A. Sánchez-Zapata, M. Moleón et J. M. Gil-Sánchez. 2008. «Current Caveats and Further Directions in the Analysis of Density-Dependent Population Regulation». *Oikos*, vol. 117, no 7, p. 1115-1119.

Chesser, R. K. et N. Ryman. 1986. «Inbreeding as a Strategy in Subdivided Populations». *Evolution*, vol. 40, no 3, p. 616-624.

Choquenot, D. 1991. «Density-Dependent Growth, Body Condition, and Demography in Feral Donkeys: Testing the Food Hypothesis». *Ecology*, vol. 72, no 3, p. 805-813.

Choudhury, S. et J. M. Black. 1994. «Barnacle Geese Preferentially Pair with Familiar Associates from Early Life». *Animal Behaviour*, vol. 48, no 1, p. 81-88.

Clark, R. G. et D. Shutler. 1999. «Avian Habitat Selection: Pattern from Process in Nest-Site Use by Ducks?». *Ecology*, vol. 80, no 1, p. 272-287.

Coleman, J. T., A. E. Coleman et D. Elphick. 1994. «Incestuous Breeding in the Mute Swan *Cygnus olor*». *Ringing & Migration*, vol. 15, no 2, p. 127-128.

Contreras-Sánchez, W. M., C. B. Schreck, M. S. Fitzpatrick et C. B. Pereira. 1998. «Effects of Stress on the Reproductive Performance of Rainbow Trout (*Oncorhynchus mykiss*)». *Biology of Reproduction*, vol. 58, no 2, p. 439-447.

Cooch, E. G., D. B. Lank, R. F. Rockwell et F. Cooke. 1989. «Long-Term Decline in Fecundity in a Snow Goose Population: Evidence for Density Dependence?». *Journal of Animal Ecology*, vol. 58, no 2, p. 711-726.

Cook, W. A., D. Cooper et D. S. Melville. 2007. «Incestuous Breeding by Sibling Variable Oystercatchers (*Haematopus unicolor*)». *Notornis*, vol. 54, no 1, p. 48.

Cooper, J. A. 1978. «The History and Breeding Biology of the Canada Geese of Marshy Point, Manitoba». *Wildlife Monographs*, vol. 61, no 61, p. 3-87.

Coulson, J. C., N. Duncan et C. Thomas. 1982. «Changes in the Breeding Biology of the Herring Gull (*Larus argentatus*) Induced by Reduction in the Size and Density of the Colony». *Journal of Animal Ecology*, vol. 51, no 3, p. 739-756.

Coulson, T., S. Albon, F. Guinness, J. Pemberton et T. Clutton-Brock. 1997. «Population Substructure, Local Density, and Calf Winter Survival in Red Deer (*Cervus Elaphus*)». *Ecology*, vol. 78, no 3, p. 852-863.

Cowan, P. J. 1973. «Parental Calls and the Approach Behavior of Young Canada Geese: A Laboratory Study». *Canadian Journal of Zoology*, vol. 51, no 6, p. 647-650.

Cresswell, W. 1994. «Flocking is an Effective Anti-Predation Strategy in Redshanks, *Tringa totanus*». *Animal Behaviour*, vol. 47, no 2, p. 433-442.

Danchin, E. et R. H. Wagner. 1997. «The Evolution of Coloniality: The Emergence of New Perspectives». *Trends in Ecology & Evolution*, vol. 12, no 9, p. 342-347.

Daniels, S. J. et J. R. Walters. 2000. «Inbreeding Depression and its Effects on Natal Dispersal in Red-Cockaded Woodpeckers». *The Condor*, vol. 102, no 3, p. 482-491.

Delestrade, A., R. H. McCleery et C. M. Perrins. 1996. «Natal Dispersal in a Heterogeneous Environment : The Case of the Great Tit in Wytham». *Acta Oecologica*, vol. 17, p. 519-529.

Dennis, D., N. North et H. Lumsden. 2000. «Range Expansion and Population Growth of Giant Canada Geese in Southern Ontario: Benefits, Drawbacks, and Management Techniques». In *Towards Conservation of the Diversity of Canada Geese (*Branta canadensis*)*, sous la dir. de K. Dickson, p. 159-165. s.l. : Canadian Wildlife Service Occasional Paper Number 103, 168p.

DeStefano, S. et R. M. DeGraaf. 2003. «Exploring the Ecology of Suburban Wildlife». *Frontiers in Ecology and the Environment*, vol. 1, no 2, p. 95-101.

Doiron, M. 2006. «Élevage et croissance des jeunes chez la bernache du Canada résidente (*Branta canadensis maxima*) dans le sud du Québec». Mémoire de maîtrise, Montréal, Université du Québec à Montréal, 67 p.

Doligez, B., C. Cadet, E. Danchin et T. Boulinier. 2003. «When to Use Public Information for Breeding Habitat Selection? The Role of Environmental Predictability and Density Dependence». *Animal Behaviour*, vol. 66, no 5, p. 973-988.

Drent, R. H. et S. Daan. 1980. «The Prudent Parent: Energetic Adjustments in Avian Breeding». *Ardea*, vol. 68, p. 225-252.

Ebensperger, L. A., M. J. Hurtado et R. Ramos-Jiliberto. 2006. «Vigilance and Collective Detection of Predators in Degus (*Octodon degus*)». *Ethology*, vol. 112, no 9, p. 879-887.

Edmands, S. 2007. «Between a Rock and a Hard Place: Evaluating the Relative Risks of Inbreeding and Outbreeding for Conservation and Management». *Molecular Ecology*, vol. 16, no 3, p. 463-475.

Einum, S., L. Sundt-Hansen et K. H Nislow. 2006. «The Partitioning of Density-Dependent Dispersal, Growth and Survival throughout Ontogeny in a Highly Fecund Organism». *Oikos*, vol. 113, no 3, p. 489-496.

Elmberg, J., K. Folkesson, M. Guillemain et G. Gunnarsson. 2009. «Putting Density Dependence in Perspective: Nest Density, Nesting Phenology, and Biome, all Matter to Survival of Simulated Mallard *Anas platyrhynchos* Nests». *Journal of Avian Biology*, vol. 40, no 3, p. 317-326.

ESRI. 2008. *ArcGIS 9.3*. Redlands : Environmental Systems Research Institute.

Ewaschuk, E. et D. A. Boag. 1972. «Factors Affecting Hatching Success of Densely Nesting Canada Geese». *Journal of Wildlife Management*, vol. 36, no 4, p. 1097-1106.

Ewen, J. G., D. P. Armstrong, K. A. Parker et P. J. Seddon. 2012. *Reintroduction Biology: Integrating Science and Management*. Oxford : Wiley-Blackwell, 499 p.

Fernández-Juricic, E., S. Siller et A. Kacelnik. 2004. «Flock Density, Social Foraging, and Scanning: An Experiment with Starlings». *Behavioral Ecology*, vol. 15, no 3, p. 371-379.

Fernandez, C., P. Azkona et J. A. Donazar. 1998. «Density-Dependent Effects on Productivity in the Griffon Vulture *Gyps fulvus*: The Role of Interference and Habitat Heterogeneity». *Ibis*, vol. 140, no 1, p. 64-69.

Ferrer, M. et I. Bisson. 2003. «Age and Territory-Quality Effects on Fecundity in the Spanish Imperial Eagle (*Aquila adalberti*)». *The Auk*, vol. 120, no 1, p. 180-186.

Ferrer, M. et J. A. Donazar. 1996. «Density-Dependent Fecundity by Habitat Heterogeneity in an Increasing Population of Spanish Imperial Eagles». *Ecology*, vol. 77, no 1, p. 69-74.

Flanagan, K. M., E. McCauley, F. Wrona et T. Prowse. 2003. «Climate Change: The Potential for Latitudinal Effects on Algal Biomass in Aquatic Ecosystems». *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 60, no 6, p. 635-639.

Flowerdew, J. R. 1974. «Field and Laboratory Experiments on the Social Behaviour and Population Dynamics of the Wood Mouse (*Apodemus sylvaticus*)». *Journal of Animal Ecology*, vol. 43, no 2, p. 499-511.

Fonseca, D. M. et D. D. Hart. 1996. «Density-Dependent Dispersal of Black Fly Neonates Is Mediated by Flow». *Oikos*, vol. 75, no 1, p. 49-58.

Forero, M. G., J. A. Donázar et F. Hiraldo. 2002. «Causes and Fitness Consequences of Natal Dispersal in a Population of Black Kites». *Ecology*, vol. 83, no 3, p. 858-872.

Forrester, G. E. et M. A. Steele. 2004. «Predators, Prey Refuges, and the Spatial Scaling of Density-Dependent Prey Mortality». *Ecology*, vol. 85, no 5, p. 1332-1342.

Francis, C. M., M. H. Richards, F. Cooke et R. F. Rockwell. 1992. «Long-Term Changes in Survival Rates of Lesser Snow Geese». *Ecology*, vol. 73, no 4, p. 1346-1362.

Fretwell, S. D. et H. L. Lucas Jr. 1970. «On Territorial Behavior and Other Factors Influencing Habitat Distribution in Birds - I. Theoretical Development». *Acta Biotheoretica*, vol. 19, no 1, p. 16-36.

García-Borboroglu, P. et P. Yorio. 2004. «Effects of Microhabitat Preferences on Kelp Gull *Larus dominicanus* Breeding Performance». *Journal of Avian Biology*, vol. 35, no 2, p. 162-169.

Gauthier, G., J. Bêty et K. A. Hobson. 2003. «Are Greater Snow Geese Capital Breeders? New Evidence from a Stable-Isotope Model». *Ecology*, vol. 84, no 12, p. 3250-3264.

Gauthier, G., J.-F. Giroux, A. Reed, A. Béchet et L. Bélanger. 2005. «Interactions Between Land Use, Habitat Use, and Population Increase in Greater Snow Geese: What Are the Consequences for Natural Wetlands?». *Global Change Biology*, vol. 11, no 6, p. 856-868.

Giroux, J.-F., J. Lefebvre, L. Bélanger, J. Rodrigue et S. Lapointe. 2001. «Establishment of a Breeding Population of Canada Geese in Southern Quebec». *Canadian Field-Naturalist*, vol. 115, p. 75-81.

Giroux, J.-F. 1981. «Use of Artificial Islands by Nesting Waterfowl in Southeastern Alberta». *Journal of Wildlife Management*, vol. 45, no 3, p. 669-679.

Greenwood, P. J. et P. H. Harvey. 1982. «The Natal and Breeding Dispersal of Birds». *Annual review of ecology and systematics*, vol. 13, p. 1-21.

Greenwood, P. J., P. H. Harvey et C. M. Perrins. 1978. «Inbreeding and Dispersal in the Great Tit». *Nature*, vol. 271, no 5640, p. 52-54.

Greenwood, P. J. 1980. «Mating Systems, Philopatry and Dispersal in Birds and Mammals». *Animal Behaviour*, vol. 28, no 4, p. 1140-1162.

Gunnarsson, G. et J. Elmberg. 2008. «Density-Dependent Nest Predation - An Experiment with Simulated Mallard Nests in Contrasting Landscapes». *Ibis*, vol. 150, no 2, p. 259-269.

Hanson, H. C. 1965. *The Giant Canada Goose*. Carbondale : Southern Illinois University Press, 225 p.

Hanson, W. C. et L. L. Eberhardt. 1971. «A Columbia River Canada Goose Population, 1950-1970». *Wildlife Monographs*, vol. 28, p. 3-61.

Harper, D. G. C. 1994. «Some Comments on the Repeatability of Measurements». *Ringing & Migration*, vol. 15, no 2, p. 84-90.

Harvey, P. W. et P. F. D. Chevins. 1987. «Crowding during Pregnancy Delays Puberty and Alters Estrous Cycles of Female Offspring in Mice». *Experientia*, vol. 43, no 3, p. 306-308.

Hestbeck, J. B. 1982. «Population Regulation of Cyclic Mammals: The Social Fence Hypothesis». *Oikos*, vol. 39, no 2, p. 157-163.

Hixon, M. A. et G. P. Jones. 2005. «Competition, Predation, and Density-Dependent Mortality in Demersal Marine Fishes». *Ecology*, vol. 86, no 11, p. 2847-2859.

Holbrook, S. J. et R. J. Schmitt. 2002. «Competition for Shelter Space Causes Density-Dependent Predation Mortality in Damselfishes». *Ecology*, vol. 83, no 10, p. 2855-2868.

Jakobsson, S. 1988. «Territorial Fidelity of Willow Warbler (*Phylloscopus trochilus*) Males and Success in Competition over Territories». *Behavioral Ecology and Sociobiology*, vol. 22, no 2, p. 79-84.

Jamieson, I. G., S. S. Taylor, L. N. Tracy, H. Kokko et D. P. Armstrong. 2009. «Why some Species of Birds Do not Avoid Inbreeding: Insights from New Zealand Robins and Saddlebacks». *Behavioral Ecology*, vol. 20, no 3, p. 575-584.

Keller, L. F. et D. M. Waller. 2002. «Inbreeding Effects in Wild Populations». *Trends in Ecology & Evolution*, vol. 17, no 5, p. 230-241.

Keller, L. F. et P. Arcese. 1998. «No Evidence for Inbreeding Avoidance in a Natural Population of Song Sparrows (*Melospiza melodia*)». *The American Naturalist*, vol. 152, no 3, p. 380-392.

Kerth, G., F. Mayer et E. Petit. 2002. «Extreme Sex-Biased Dispersal in the Communally Breeding, Nonmigratory Bechstein's Bat (*Myotis bechsteinii*)». *Molecular Ecology*, vol. 11, no 8, p. 1491-1498.

Kim, S. Y., R. Torres et H. Drummond. 2009. «Simultaneous Positive and Negative Density-Dependent Dispersal in a Colonial Bird Species». *Ecology*, vol. 90, no 1, p. 230-239.

Klint, T. 1978. «Significance of Mother and Sibling Experience for Mating Preferences in the Mallard (*Anas platyrhynchos*)». *Zeitschrift für Tierpsychologie*, vol. 47, no 1, p. 50-60.

Korpimäki, E. 1993. «Regulation of Multiannual Vole Cycles by Density-Dependent Avian and Mammalian Predation?». *Oikos*, vol. 66, no 2, p. 359-363.

Lack, D. L. 1967. *The Natural Regulation of Animal Numbers*. Oxford : Oxford University Press, 343 p.

Lambin, X. 1994. «Natal Philopatry, Competition for Resources, and Inbreeding Avoidance in Townsend's Voles (*Microtus Townsendii*)». *Ecology*, vol. 75, no 1, p. 224-235.

Larivière, S. et F. Messier. 1998. «Effect of Density and Nearest Neighbours on Simulated Waterfowl Nests: Can Predators Recognize High-Density Nesting Patches?». *Oikos*, vol. 83, no 1, p. 12-20.

Leafloor, J. O. 1998. «Philopatry, Geographic Variation in Body Size, and Genetic Structure of Canada Geese». Thèse de doctorat, Madison, University of Wisconsin, 109 p.

Léna, J. P., J. Clobert, M. de Fraipont, J. Lecomte et G. Guyot. 1998. «The Relative Influence of Density and Kinship on Dispersal in the Common Lizard». *Behavioral Ecology*, vol. 9, no 5, p. 500-507.

Lepage, D., G. Gauthier et A. Reed. 1998. «Seasonal Variation in Growth of Greater Snow Goose Goslings: The Role of Food Supply». *Oecologia*, vol. 114, no 2, p. 226-235.

Lessells, C. M. et P. T. Boag. 1987. «Unrepeatable Repeatabilities: A Common Mistake». *The Auk*, vol. 104, no 1, p. 116-121.

Lessels, C. M. 1985. «Natal and Breeding Dispersal of Canada Geese *Branta canadensis*». *Ibis*, vol. 127, no 1, p. 31-41.

Liberg, O., H. Andrén, H. C. Pedersen, H. Sand, D. Sejberg, P. Wabakken, M. Åkesson et S. Bensch. 2005. «Severe Inbreeding Depression in a Wild Wolf *Canis lupus* Population». *Biology Letters*, vol. 1, no 1, p. 17-20.

Lode, T. 2000. «Functional Response and Area-Restricted Search in a Predator: Seasonal Exploitation of Anurans by the European Polecat, *Mustela putorius*». *Austral Ecology*, vol. 25, no 3, p. 223-231.

MacInnes, C. D. 1966. «Population Behavior of Eastern Arctic Canada Geese». *Journal of Wildlife Management*, vol. 30, no 3, p. 536-553.

Marchand, M. N. et J. A. Litvaitis. 2004. «Effects of Landscape Composition, Habitat Features, and Nest Distribution on Predation Rates of Simulated Turtle Nests». *Biological Conservation*, vol. 117, no 3, p. 243-251.

Marzluff, J. M. et R. Sallabanks. 1998. *Avian Conservation: Research and Management.* Washington : Island Press, 563 p.

McCormick, M. I. 1998. «Behaviorally Induced Maternal Stress in a Fish Influences Progeny Quality by a Hormonal Mechanism». *Ecology*, vol. 79, no 6, p. 1873-1883.

McPeek, M. A., N. L. Rodenhouse, R. T. Holmes et T. W. Sherry. 2001. «A General Model of Site-Dependent Population Regulation: Population-Level Regulation Without Individual-Level Interactions». *Oikos*, vol. 94, no 3, p. 417-424.

Murray, Bertram G Jr. 1967. «Dispersal in Vertebrates». *Ecology*, vol. 48, no 6, p. 975-978.

Nakadate, M., T. Shikano et N. Taniguchi. 2003. «Inbreeding Depression and Heterosis in Various Quantitative Traits of the Guppy, *Poecilia reticulata*». *Aquaculture*, vol. 220, no 1, p. 219-226.

Negro, J. J., F. Hiraldo et J. A. Donazar. 1997. «Causes of Natal Dispersal in the Lesser Kestrel: Inbreeding Avoidance or Resource Competition?». *Journal of Animal Ecology*, vol. 66, no 5, p. 640-648.

Nelson, H. et R. Oetting. 1998. «Giant Canada Goose Flocks in the United States». In *Biology and Management of Canada Geese*, sous la dir. de D. H. Rush, M. D. Samuel, D. D. Humburg et B. D. Sullivan, p. 483-495. Milwaukee : Proceedings of the international Canada goose symposium.

Nephew, B. C. et L. Romero. 2003. «Behavioral, Physiological, and Endocrine Responses of Starlings to Acute Increases in Density». *Hormones and Behavior*, vol. 44, no 3, p. 222-232.

Nilsson, J. A. 1989. «Causes and Consequences of Natal Dispersal in the Marsh Tit, *Parus palustris*». *Journal of Animal Ecology*, vol. 58, no 2, p. 619-636.

Nilsson, L. et H. Persson. 2001. «Natal and Breeding Dispersal in the Baltic Greylag Goose *Anser anser*». *Wildfowl*, vol. 52, p. 21-30.

Owen, M. et J. M. Black. 1991. «A Note on Migration Mortality and its Significance in Goose Populations Dynamics». *Ardea*, vol. 79, no 2, p. 195-196.

Owen, M., J. M. Black et H. Liber. 1988. «Pair Bond Duration and Timing of its Formation in Barnacle Geese (*Branta leucopsis*)». In *Waterfowl in Winter*, sous la dir. de M. W. Weller, p. 23-38. Minneapolis: University of Minnesota.

Pannetier Lebeuf, A. et J.-F. Giroux. En préparation. «Density-Dependent Effects on Reproductive Success of Temperate-Nesting Canada Geese».

Pannetier Lebeuf, A. et J.-F. Giroux. 2013. «Sibling Pairing in Temperate-Nesting Canada Geese». *Wilson Journal of Ornithology*, sous presse.

Paradis, E., S. R. Baillie, W. J. Sutherland et R. D. Gregory. 1998. «Patterns of Natal and Breeding Dispersal in Birds». *Journal of Animal Ecology*, vol. 67, no 4, p. 518-536.

Parker, M. W., S. W. Kress, R. T. Golightly, H. R. Carter, E. B. Parsons, S. E. Schubel, J. A. Boyce, G. J. McChesney et S. M. Wisely. 2007. «Assessment of Social Attraction Techniques Used to Restore a Common Murre Colony in Central California». *Waterbirds*, vol. 30, no 1, p. 17-28.

Part, T. 1990. «Natal Dispersal in the Collared Flycatcher: Possible Causes and Reproductive Consequences». *Ornis Scandinavica*, vol. 21, no 2, p. 83-88.

Pasinelli, G. et J. R. Walters. 2002. «Social and Environmental Factors Affect Natal Dispersal and Philopatry of Male Red-Cockaded Woodpeckers». *Ecology*, vol. 83, no 8, p. 2229-2239.

Pasinelli, G., K. Schiegg et J. R. Walters. 2004. «Genetic and Environmental Influences on Natal Dispersal Distance in a Resident Bird Species». *The American Naturalist*, vol. 164, no 5, p. 660-669.

Penteriani, V., J. Balbontin et M. Ferrer. 2003. «Simultaneous Effects of Age and Territory Quality on Fecundity in Bonelli's Eagle *Hieraaetus fasciatus*». *Ibis*, vol. 145, no 2, p. E77-E82.

Picman, J., S. Pribil, A. Isabelle et A. Powell. 2002. «Antipredation Value of Colonial Nesting in Yellow-Headed Blackbirds». *The Auk*, vol. 119, no 2, p. 461-472.

Pilotte, C. 2012. «Survie annuelle des Bernaches du Canada établies dans le sud du Québec». Mémoire de maîtrise, Montréal, Université du Québec à Montréal, 61 p.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar et R Development Core Team. 2012. *Nlme: Linear and Nonlinear Mixed Effects Models.* R package version 3.1-104.

Pöysä, H., J. Elmberg, K. Sjöberg et P. Nummi. 1998. «Habitat Selection Rules in Breeding Mallards (*Anas platyrhynchos*): A Test of Two Competing Hypotheses». *Oecologia*, vol. 114, no 2, p. 283-287.

Pulliam, H. R. et B. J. Danielson. 1991. «Sources, Sinks, and Habitat Selection: A Landscape Perspective on Population Dynamics». *American Naturalist*, vol. 137, no Suppl, p. S50-S66.

R Core Team. 2012. *R: A Language and Environment for Statistical Computing*. Vienna. ISBN 3-900051-07-0.

Radesäter, T. 1976. «Individual Sibling Recognition in Juvenile Canada Geese (*Branta canadensis*)». *Canadian Journal of Zoology*, vol. 54, no 7, p. 1069-1072.

Rave, E. H., R. C. Fleischer, F. Duvall et J. M. Black. 1998. «Factors Influencing Reproductive Success in Captive Populations of Hawaiian Geese *Branta sandvicensis*». *Wildfowl*, vol. 49, p. 36-44.

Ringelman, K. M., J. M. Eadie et J. T. Ackerman. 2012. «Density-Dependent Nest Predation in Waterfowl: The Relative Importance of Nest Density Versus Nest Dispersion». *Oecologia*, vol. 169, no. 3, p. 695-702.

Rockwood, L. L. 2009. *Introduction to Population Ecology*. Malden : Blackwell Publishing, 352 p.

Rodenhouse, N. L., T. S. Sillett, P. J. Doran et R. T. Holmes. 2003. «Multiple Density-Dependence Mechanisms Regulate a Migratory Bird Population during the Breeding Season». *Proceedings of the Royal Society B: Biological Sciences*, vol. 270, no 1529, p. 2105-2110.

Rodenhouse, N. L., T. W. Sherry et R. T. Holmes. 1997. «Site-Dependent Regulation of Population Size: A New Synthesis». *Ecology*, vol. 78, no 7, p. 2025-2042.

Running, S. W., R. R. Nemani, F. A. Heinsch, M. Zhao, M. Reeves et H. Hashimoto. 2004. «A Continuous Satellite-Derived Measure of Global Terrestrial Primary Production». *BioScience*, vol. 54, no 6, p. 547-560.

Ruusila, V., H. Pöysä et P. Runko. 2001. «Costs and Benefits of Female-Biased Natal Philopatry in the Common Goldeneye». *Behavioral Ecology*, vol. 12, no 6, p. 686-690.

Saino, N., M. Romano, R. P. Ferrari, R. Martinelli et A. P. Møller. 2005. «Stressed Mothers Lay Eggs with High Corticosterone Levels which Produce Low-Quality Offspring». *Journal of Experimental Zoology Part A: Comparative Experimental Biology*, vol. 303A, no 11, p. 998-1006.

Salvante, K. G. et T. D. Williams. 2003. «Effects of Corticosterone on the Proportion of Breeding Females, Reproductive Output and Yolk Precursor Levels». *General and Comparative Endocrinology*, vol. 130, no 3, p. 205-214.

Sand, H., R. Bergström, G. Cederlund, M. Östergren et F. Stålfelt. 1996. «Density-Dependent Variation in Reproduction and Body Mass in Female Moose *Alces alces*». *Wildlife Biology*, vol. 2, no 4, p. 233-245.

Sedinger, J. S., M. P. Herzog, B. T. Person, M. T. Kirk, T. Obritchkewitch, P. P. Martin et A. A. Stickney. 2001. «Large-Scale Variation in Growth of Black Brant Goslings Related to Food Availability». *The Auk*, vol. 118, no 4, p. 1088-1095.

Sedinger, J. S., M. S. Lindberg, B. T. Person, M. W. Eichholz, M. P. Herzog et P. L. Flint. 1998. «Density-Dependent Effects on Growth, Body Size, and Clutch Size in Black Brant». *Auk*, vol. 115, no 3, p. 613-620.

Serrano, D., M. G. Forero, J. A. Donázar et J. L. Tella. 2004. «Dispersal and Social Attraction Affect Colony Selection and Dynamics of Lesser Kestrels». *Ecology*, vol. 85, no 12, p. 3438-3447.

Sheriff, M. J., C. J. Krebs et R. Boonstra. 2009. «The Sensitive Hare: Sublethal Effects of Predator Stress on Reproduction in Snowshoe Hares». *Journal of Animal Ecology*, vol. 78, no 6, p. 1249-1258.

Shields, W. M. 1982. *Philopatry, Inbreeding, and the Evolution of Sex*. Albany : State University of New York Press, 245 p.

Silverin, B. 1998. «Behavioural and Hormonal Responses of the Pied Flycatcher to Environmental Stressors». *Animal Behaviour*, vol. 55, no 6, p. 1411-1420.

Sovey, S. J. et I. J. Ball. 1998. «Influence of Island Size on Number and Success of Canada Goose Nests in Northwestern Montana». In *Biology and Management of Canada Geese*, sous la dir. de D. H. Rush, M. D. Samuel, D. D. Humburg et B. D. Sullivan, p. 43-46. Milwaukee : Proceedings of the international Canada goose symposium.

Stamps, J. A. 1987. «Conspecifics as Cues to Territory Quality: A Preference of Juvenile Lizards (*Anolis aeneus*) for Previously Used Territories». *The American Naturalist*, vol. 129, no 5, p. 629-642.

Stamps, J. A. 1988. «Conspecific Attraction and Aggregation in Territorial Species». *The American Naturalist*, vol. 131, no 3, p. 329-347.

Stewart, K., R. Bowyer, B. Dick, B. Johnson et J. Kie. 2005. «Density-Dependent Effects on Physical Condition and Reproduction in North American Elk: An Experimental Test». *Oecologia*, vol. 143, no 1, p. 85-93.

Stier, K. S., B. Almasi, J. Gasparini, R. Piault, A. Roulin et L. Jenni. 2009. «Effects of Corticosterone on Innate and Humoral Immune Functions and Oxidative Stress in Barn Owl Nestlings». *Journal of Experimental Biology*, vol. 212, no 13, p. 2085-2091.

Sullivan, B. D. et J. J. Dinsmore. 1990. «Factors Affecting Egg Predation by American Crows». *Journal of Wildlife Management*, vol. 54, no 3, p. 433-437.

Surrendi, D. C. 1970. «The Mortality, Behavior, and Homing of Transplanted Juvenile Canada Geese». *Journal of Wildlife Management*, vol. 34, no 4, p. 719-733.

Sutherland, W. J. 1996. *From Individual Behaviour to Population Ecology*. Oxford : Oxford University Press, 213 p.

Szulkin, M. et B. C. Sheldon. 2008a. «Correlates of the Occurrence of Inbreeding in a Wild Bird Population». *Behavioral Ecology*, vol. 19, no 6, p. 1200-1207.

Szulkin, M. et B. C. Sheldon. 2008b. «Dispersal as a Means of Inbreeding Avoidance in a Wild Bird Population». *Proceedings: Biological Sciences*, vol. 275, no 1635, p. 703-711.

Török, J. et L. Tóth. 1988. «Density Dependence in Reproduction of the Collared Flycatcher (*Ficedula albicollis*) at High Population Levels». *Journal of Animal Ecology*, vol. 57, no 1, p. 251-258.

U.S. Fish and Wildlife Service. Division on Migratory Bird Management. 2005. *Resident Canada Goose Management: Environmental Impact Statement*. Arlington : U.S. Fish and Wildlife Service.

Walter, S. E. et D. H. Rusch. 1997. «Accuracy of Egg Flotation in Determining Age of Canada Goose Nests». *Wildlife Society Bulletin*, vol. 25, no 4, p. 854-857.

Ward, M. P. et S. Schlossberg. 2004. «Conspecific Attraction and the Conservation of Territorial Songbirds». *Conservation Biology*, vol. 18, no 2, p. 519-525.

Warren, S. M., A. D. Fox, A. Walsh et P. O'Sullivan. 1993. «Extended Parent-Offspring Relationships in Greenland White-Fronted Geese (*Anser albifrons flavirostris*)». *The Auk*, vol. 110, no 1, p. 145-148.

Waser, P. M. 1985. «Does Competition Drive Dispersal?». *Ecology*, vol. 66, no 4, p. 1170-1175.

Wauters, L. A. et L. Lens. 1995. «Effects of Food Availability and Density on Red Squirrel (*Sciurus Vulgaris*) Reproduction». *Ecology*, vol. 76, no 8, p. 2460-2469.

Wheelwright, N. T. et R. A. Mauck. 1998. «Philopatry, Natal Dispersal, and Inbreeding Avoidance in an Island Population of Savannah Sparrows». *Ecology*, vol. 79, no 3, p. 755-767.

Wheelwright, N. T., C. R. Freeman-Gallant et R. A. Mauck. 2006. «Asymmetrical Incest Avoidance in the Choice of Social and Genetic mates». *Animal Behaviour*, vol. 71, no 3, p. 631-639.

Wiklund, C. G. 1996. «Determinants of Dispersal in Breeding Merlins (*Falco Columbarius*)». *Ecology*, vol. 77, no 6, p. 1920-1927.

Wilkin, T. A., D. Garant, A. G. Gosler et B. C. Sheldon. 2006. «Density Effects on Life-History Traits in a Wild Population of the Great Tit *Parus major*: Analyses of Long-Term Data with GIS Techniques». *Journal of Animal Ecology*, vol. 75, no 2, p. 604-615.

Williams, T. D., E. G. Cooch, R. L. Jefferies et F. Cooke. 1993. «Environmental Degradation, Food Limitation and Reproductive Output: Juvenile Survival in Lesser Snow Geese». *Journal of Animal Ecology*, vol. 62, no 4, p. 766-777.

Zanette, L. 2002. «What Do Artificial Nests Tells Us about Nest Predation?». *Biological Conservation*, vol. 103, no 3, p. 323-329.

Zicus, M. C. 1981a. «Canada Goose Brood Behavior and Survival Estimates at Crex Meadows, Wisconsin». *The Wilson Bulletin*, vol. 93, no 2, p. 207-217.

Zicus, M. C. 1981b. «Molt Migration of Canada Geese from Crex Meadows, Wisconsin». *Journal of Wildlife Management*, vol. 45, no 1, p. 54-63.